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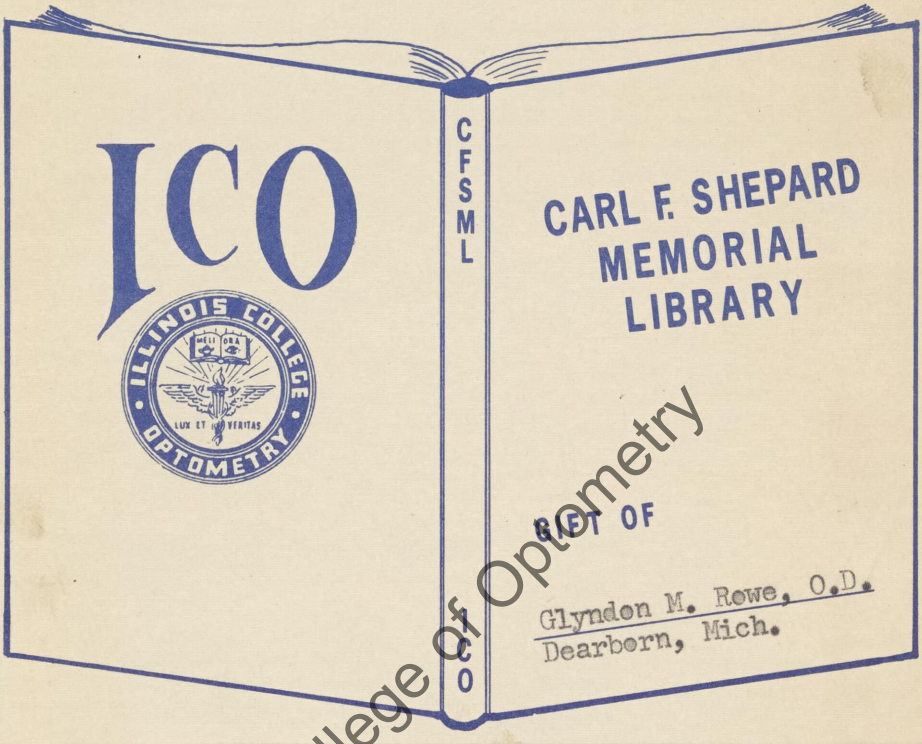


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# INTRODUCTION TO THE STUDY

OF THE

# ANATOMY AND PHYSIOLOGY

# OF THE EYE

By Dr. MAX COQUE, B.Sc.

(*Principal of the British Optical Institute*).

WITH A FOREWORD BY

Mr. J. H. SUTCLIFFE, O.B.E., F.Inst.P.

(*Secretary of the British Optical Association*).

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# FOREWORD.

TO all those interested in the education and advancement of the optical practitioner this book, by Dr. Max Coque, needs but little recommendation. Written, as it has been, with the object of bridging the gulf between the student's elementary text-books and more advanced optical treatises, it fills a conspicuous gap in the technical equipment of the present-day optician. The aspirant to ordinary research work will find in this book minute instructions for the making of microscopic sections, and for the dissection of an eye; the student of the nervous apparatus of vision will learn much from the admirable handling of this subject, while the lucid descriptions devoted to the anatomy of the eye and of the orbit will strongly appeal to the beginner.

Few men can be so well equipped as Dr. Coque for the authorship of this book. His interest in optical work dates back to the days when, as assistant to Professor Monoyer (of Dioptre fame), he initiated the medical students of the University of Lyons into the intricacies of physiologic optics. As clinical assistant to the late Dr. Dor (Professor of Ophthalmology) he increased that fund of knowledge, which later he was to share with his pupils in England. So many generations of students have studied under his guidance, that it is probably safe to say that there is hardly a town of any size in any English-speaking country where his name is not known to at least one optician. Although chiefly confined to the education

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of his students, his activities have included, amongst others, the authorship of papers on "The Evolution of the Eye in the Zoological Series," "The Production of Light by Living Beings" (read to the Optical Society, November, 1912), "The Study of Mathematics" (read to the Optical Convention, 1912), "Radiation, Illumination and Colour," "Fundamental Principles and Technique of Perimetry," "Retinoscopy," "Magnification by Optical Instruments," etc.

With steady persistence Dr. Max Coque has laboured earnestly and patiently for twenty-five years to assist opticians, not only those of Great Britain but of all parts of the world, to increase their efficiency, and I sincerely hope this Foreword will stimulate the Reader to increase his store of knowledge from the pages of this work.

J. H. SUTCLIFFE.

Clifford's Inn Hall,
London. 1927.

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# AUTHOR'S PREFACE.

THE law has imposed upon the optician the responsibility of recognising the presence of disease in the eye. In the case of Markham versus Thomas (1909) damages were directed to be paid to plaintiff on the ground that the optician had failed to notice the presence of a pathological condition namely, Conical Cornea. This legal responsibility has never been set aside and the judgment referred to just now might well form a precedent and be the basis of similar judgments in cases of the same kind.

For this reason, the Council of the British Optical Association has very wisely introduced the subject of Recognition of Ocular Diseases into the syllabus of the F.B.O.A. Examination. Now, the recognition of pathological ocular conditions, apart from any attempt at treatment (which is the lawful province of the ophthalmic surgeon) necessitates on the part of the optician a sufficient knowledge not only of the Anatomy and Physiology of the Eye itself but of the main laws of General Physiology, i.e., of the processes, the result of which constitute life, and also of the mechanism of the most important pathological processes, which, as we shall see, are but exaggerations of normal or physiological processes.

The present work has been undertaken to provide the optical student with a sufficiently full description of the anatomical structure of the eye, together with

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enough details of general anatomy and physiology, and of the most frequently observed pathological processes.

Whilst much may be learned of anatomy from careful study of diagrammatic drawings, as found in most text-books, and also from the dissection of a fresh eye, such as that of the pig or the ox, yet experience has shown that the student often gets a wrong impression from the mere examination of diagrams; beside, in dissection, a previous hardening of the specimen employed is usually necessary to obtain a satisfactory view of the structures involved.

It is obvious however that, so far as the study of the human eye is concerned, the ideal way is to examine different sections of such an eye. But the average student would find it impossible to procure the necessary material for a work of this kind, and for this reason the author is most grateful to have obtained from the Clarendon Press permission to reproduce twelve of the beautiful stereoscopic views of the interior of the eye, which have been prepared under the supervision of Dr. Arthur Thomson, Professor of Human Anatomy at the University of Oxford. The set of Dr. Thomson's plates was intended as illustration for a course of lectures he delivered to graduates preparing for the Diploma of Ophthalmology of the Oxford University. The complete set goes beyond the requirements of the students for whom the present book is written, but we have selected a series of plates the reproduction of which will prove most useful.

As Dr. Thomson remarks in the preface of the booklet accompanying his set, many of the structures of the human eye are so small that it is only possible under ordinary circumstances to obtain a satisfactory

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view of them by the use of a magnifying glass. This usually involves their examination by monocular vision and consequently entails a loss of that stereoscopic effect which is so necessary to determine their exact relation. With the object of overcoming this defect, preparations were made under Dr. Thomson's supervision in such a way as to preserve the stereoscopic effect and at the same time to provide for such a magnification as would render clear most of the details desired. In some instances a millimetre scale is photographed alongside the preparation, so that the student may have some approximate idea of the size of the structures he is viewing.

It is not suggested by Dr. Thomson that his full set of stereoscopic pictures should be a substitute for the experience gained by actual dissection, and the same remark applies even more forcibly to the few plates which we have reproduced and we place now before the student. But when one considers that the necessary material, more especially if of human nature, is difficult to procure in a sufficiently fresh condition to display all the details of structure, it becomes obvious that the accompanying plates may serve as a reminder of features previously examined and may prove useful as a handy means of reference when permanent preparations or museum specimens are not readily available.

In most instances, the specimens from which Dr. Thomson's photographs were taken were removed within four hours after death. They were hardened in a four per cent. solution of formol, subsequently frozen and then cut. The further dissections which were necessary were then performed and the preparation photographed under spirit. The result is perfect,

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as can be seen from twelve of the stereograms accompanying the present book, which are exact photographic reproductions of Dr. Thomson's original set. No doubt the more delicate structures undergo some alterations in the hardening process, but the same may be said of all other methods of preparation that have been suggested.

The original set of stereoscopic pictures, published by Dr. Thomson in 1912, is intended to be used by students familiar with the Anatomy of the Eye and the plates (65 in number) are grouped according to the method of section employed, or as illustrative of different stages in a dissection. For this reason, the booklet accompanying the set is divided into five chapters dealing with (1) Antero-posterior sections; (2) Dissection of the eye from the front; (3) Anterior half of the eye seen from behind; (4) The lens; and (5) The posterior half of the eye.

Our purpose is somewhat different and while the reader is supposed from the outset to have a slight knowledge of the structure of the ocular globe, which may be derived from a careful reading of any elementary text-book, we shall proceed to a study of the Anatomy of the Eye by describing successively the various coats and media which constitute the organ of sight.

The stereoscopic plates, the reproduction of which has been allowed by the Clarendon Press, have been photographed by the Camerascope Co., and are supplied with a convenient folding model of stereoscope, though any other form of stereoscope could be used.

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We wish to record once more our sincerest thanks to the Clarendon Press for permission to reproduce some of the original plates of Dr. Thomson. We also wish to thank the Camerascope Co. for their excellent reproduction, and especially the Publishers, Messrs. J. & R. Fleming, Ltd., who have taken a great interest in our work and have made it possible to place it before the student.

The writer of this book has no pretention to originality. A practice of teaching extending over a period of more than twenty-five years, both on the Continent and in this country, has shown him the difficulty experienced by the student who starts on the study of the anatomy of the eye. Many of the diagrams and illustrations found in most text-books on the subject do not give him a clear idea of the real arrangement of the various parts of the human eye, and it is chiefly for this reason that the author is particularly thankful for permission to reproduce some of Dr. Thomson's plates, the examination of which by means of a stereoscope affords a life-like and solid appearance of the structures under investigation. Beside the twelve stereoscopic plates reproduced from Dr. Thomson's set, we have added two more stereoscopic photographs, one of the orbital cavity and one of a section of the skull showing the orbits and the accessory cavities in communication with the orbits. These two plates are not intended to do away with an examination of a skull but they show details of structure which would not be easily recognised on ordinary drawings.

The present work has mainly been written from the author's own notes of his lectures delivered to

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students attending the British Optical Institute. In the introductory chapters devoted to a brief study of what is necessary of general anatomy, general physiology and pathology, the writer has borrowed freely from standard books, especially the admirable "Lessons in Elementary Physiology" of Huxley, and from Dr. Forrest's book on "Recognition of Ocular Diseases"; the latter work being the first attempt ever made to enable the optical student to arrive at a clear understanding of the most frequently observed pathological conditions of the eye.

The author wishes to draw the student's attention to the chapters devoted to the Nervous Apparatus of the Eye, a subject which, in his opinion, has never been given in a form adapted to the requirements of readers not acquainted with medical work. A special chapter deals with the Technique of Dissection and Microscopic Section Making, and another one with the Methods of Examination of the Living Eye, which are of use in the study of the anatomical structure of the globe, especially that of the anterior part, by direct examination or with the help of a magnifying glass or with a short focus telescope, acting as a comparatively low power microscope. Focal illumination and the use of the slit lamp are dealt with in the same chapter.

A glossary of many anatomical, physiological and pathological terms which may not be explicitly defined in the book, contains also a sufficient account of some important points in physical and natural science that have a strong bearing on our subject. An alphabetical index for reference purposes, completes the book.

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In a work of this kind, the various parts of which are more or less intimately connected, repetitions are almost unavoidable. As a matter of fact, the writer has not attempted to avoid entirely such repetitions which, in his mind, are calculated to emphasise the most important points and their interconnections in a somewhat intricate subject.

To enable the student to arrive at a clear understanding of the matter contained in this book, it is suggested that, at a first reading, certain portions of the text be left over. These portions are indicated by a vertical line in the margin. When a general view of the subject has thus been obtained from the study of the parts not so marked, the reader should revert to the marginally lined portions to complete his study.

Apart from the stereoscopic plates alluded to above, the book itself is illustrated by diagrams many of which are original, while a few are reproduced from standard books.

Though the main part of the book is devoted to the Anatomy and Physiology of the Human Eye, frequent remarks on comparative anatomy will be of some help.

If the author has succeeded in interesting his readers in a fascinating study and if he is instrumental in getting some of them to carry on their work a step further by means of more complete books which are not adapted to the needs of a comparative beginner and thus to acquire the knowledge that is necessary to raise the work of the ophthalmic optician to a

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professional level, he will be amply rewarded for the time he has had to spend in compiling this book.

The writer particularly wishes to acknowledge what he owes to his assistant, Mr. G. Colebrook, F.B.O.A. (Honours), F.S.M.C. (Master's Prizeman), whose many suggestions have proved most useful and who has given him, in the preparation of the book generally, in the drawing of the diagrams, and in the compilation of the glossary and of the index, the same valuable help as he gives him daily in the teaching work of the Institute.

M. C.

Fern Lodge,
Grove Road,
London, S.W.9.

*May*, 1927.

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# CHAPTER I.

## PHYSIOLOGICAL WORK AND GENERAL ARRANGEMENT OF THE VARIOUS PARTS OF THE LIVING BODY. LIVING TISSUES.

**The Physiological Work of the Living Body Generally.**

The eye is a living organ, a part of a living body which, apart from the purely optical defects, or errors of refraction it may present, may be affected by various pathological conditions whose seat is in a portion of the body more or less remote from the eye itself. Well known instances are the poisoning of the optic nerve due to excessive use of tobacco or alcohol (toxic amblyopia); the peculiar form of cataract or lens opacity due to diabetes; the iritis (or inflammation of the iris) as a consequence of rheumatism; the form of retinitis (albuminuric retinitis) due to Bright's disease; the inflammation of the optic nerve head caused by a cerebral tumour.

It is not rare for an optician to observe, in a careful ophthalmoscopic examination, the first appearance of albuminuric retinitis or of optic neuritis when the morbid process causing a loss or a reduction of visual acuity has not yet reached a degree which attracts otherwise the subject's attention, and in such cases it is, of course, the duty of the optician to refer the subject to a medical man, who will take the necessary measures to deal with the root of the matter. It follows from this that, apart from the legal responsibility imposed upon the optician by the judgment in the case of Markham versus Thomas, which has been referred to in the preface to this work, it is imperative for him to be able to arrive at a true understanding of the main points in the physiological work of the body generally inasmuch as they bear on the functions and on the health of the organ of sight.

With this purpose in view, the main portion of the present book, concerned with the Anatomy of the Eye, is prefaced by a short account of Elementary Physiology and of the more frequently observed pathological processes.

Modern science has established on a sound basis the fact that the physiological work of the body is comparable to that of a machine, and that the development of energy or the capability of producing work with which the human body as well as that of all other living beings is endowed, is governed by the physical law termed the Law of Conservation of Energy. This law, together with the Law of Conservation or Indestructibility of Matter, which has been



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established by eminent chemists (Lavoisier, Dalton, etc.) towards the end of the 18th and the beginning of the 19th centuries, constitutes the fundamental basis of both physical and physiological science.

The human body may be regarded as a machine, the fuel being the food which undergoes oxidation, thus producing heat and the necessary energy for muscular and nervous labour. The food is not only an energy producer, but it also furnishes the materials for the repair of the waste that is continually going on and, at least during the early period of life, it supplies the materials for the increase in the size of the body and of its various parts or organs. In fact, the body is not only a machine but is a self-repairing and a self-constructing machine.

Though it is difficult to give a satisfactory definition of life, yet it is a matter of observation that the human body (and the same applies to the body of any living animal) constantly performs a great diversity of actions, some of which are obvious, some others are more difficult to observe, while others again can be detected only by the use of the most delicate scientific appliances.

As Huxley puts it: "Some parts of the body of a living man are plainly always in motion. Even in sleep, the constant rise and fall of the chest remind us that we are viewing slumber and not death. A more careful observation is needed to detect the motion of the heart or the pulsation of the arteries, or again, to ascertain the changes in the size of the pupil of the eye with varying light, or to recognise that the air which is breathed out of the body is hotter, damper and richer in carbonic acid gas than the air which is taken in by breathing. Lastly, when we try to find out what happens in the eye when that organ is adapted to different distances, or what happens in a nerve when it is excited, or in virtue of what mechanism a sudden pain makes one start, we have to call into operation all the resources of physics and chemistry, and all the methods of inductive and deductive logic."

A general examination of the human body or of the body of any of the higher animals shows that it is made of different parts easily separable, such as the limbs, the head, the brain, the heart, the lungs, etc. Each of these parts has a definite work or function to perform in the economy of the body generally.

A fundamental fact in the physiological work of the body is that this work implies absorption of oxygen, of water and food, together with elimination of waste products.

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The organs which convert food into nutrient material in a soluble and assimilable form, are the organs of alimentation (or the alimentary canal). Those which distribute nutriment to the various parts in which it is required are the circulatory organs, and those which serve to get rid of the waste products are the organs of excretion. We cannot do more in this book than to give a very brief account of the general arrangement of these organs, and of the main physiological work of the body[1].

The organs of alimentation consist of the alimentary canal (mouth, pharynx, gullet or œsophagus, stomach and intestines), together with their annexes or appendages. What they do is first to receive and grind the food, then they act upon it with chemical agents of which they possess a store which is renewed as fast as it is used. In this way they convert the food into a fluid containing nutritious matter in solution or suspension, which is absorbed in the blood stream, and non-nutritious dregs which will be eliminated. This process, i.e., the work of the alimentary organs, is termed digestion.

The distribution of the nutritious material resulting from the process of digestion is carried out by means of the circulatory organs. A system of minute tubes, termed capillaries, is arranged through the whole organism except the epidermis, the cartilages, the substance of the teeth and a few other parts, for instance, the cornea and the crystalline lens of the eye. On both sides these tubes pass into others which are called arteries and veins respectively, which, after becoming larger and larger, finally open in the heart, an organ which, as we know, is placed in the thorax or cavity of the chest. During life these tubes, as well as the chambers of the heart with which they are connected, are filled with a liquid which is the red fluid we are all familiar with as blood. The walls of the heart are muscular and contract rhythmically, i.e., at regular intervals. In fact, the heart, by means of the contraction of its walls, acts as a pump, driving the blood into the arteries and thence into the

[1] What is said in the following pages on the physiological work of the body should not be regarded as being a complete study of the subject, but a mere introduction to it, which the student should supplement by referring to Huxley's Lessons in Elementary Physiology, published by Messrs. Macmillan & Co., Ltd. A simpler work is Sir Michael Foster's Physiology belonging to the Science Primers Series, also published by Macmillan & Co., Ltd. Those students who wish to go a step further, and acquire a sound knowledge of Physiology, will find all the material they require in Sir Michael Foster's Text Book of Physiology (published by Messrs. Macmillan), or in Starling's Principles of Human Physiology, published by Churchill. The last two works are, however, somewhat difficult to read without an elementary knowledge of the subject, and it is with the hope that the first few chapters of the present book may form an introduction to these more complete works that they have been compiled.

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capillaries, whence it returns by the veins back to the heart. This is the circulation of the blood.

The fluid containing the dissolved or suspended nutritive materials which are the result of the process of digestion, traverses the very thin layer of soft and permeable tissue which separates the cavity of the alimentary canal from the cavities of the innumerable capillary vessels which lie in the walls of that canal, and so enters the blood with which the capillaries are filled. Whirled away by the stream of the circulation, the blood thus loaded with nutriment, enters the heart, and is thence propelled into all parts of the body. To these parts it supplies the nutriment they require, and from them it takes the waste products and finally returns to the heart through the veins loaded with useless and injurious excretions which sooner or later take the form of water, carbonic acid gas and urea.

These excretory products are separated from the blood by the work of the excretory organs, of which there are three, namely, the skin, the lungs, and the kidneys. Different as these organs may be in appearance, all are built on the same principle. Each, in ultimate analysis, is made of a very thin sheet of tissue like a delicate blotting paper, the one face of which is free or lines a cavity communicating with the exterior, while the other is in contact with the blood which has to be purified. The excreted matters are, as it were, strained from the blood through this delicate layer of tissue on its free surface, whence they make their escape.

Each of the three excretory organs is especially concerned with the elimination of one of the main waste products—water, carbonic acid gas and urea—though it may at the same time be a means of escape for the other two. Thus, the lungs especially serve to the elimination of carbonic acid gas, but they also give off a good deal of water in the form of steam. The duty of the kidneys is to excrete urea, but they also eliminate a large quantity of water and a slight amount of carbonic acid gas dissolved in water. The skin gives off much water in the form of vapour, a little carbonic acid gas and a certain quantity of saline matter with perhaps a trace of urea. The lungs, or more generally the respiratory organs, play a double part. Not only do they eliminate excretory products as we saw just now, but they import in the economy a substance which is neither food nor drink, though it is as important as either, to wit, oxygen. It has been ascertained by chemists that the waste products leaving the body through the organs of excretion contain more oxygen than the food and water which are taken in. Exactly as carbonic acid gas and water are passing

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from the blood into the external air through the lungs, oxygen is passing from the air into the blood through the lungs, and is thus carried by the blood to all parts of the body. The chemical action of the oxygen thus carried to all parts, goes on continually. All parts of the body are continually being oxidised, i.e., burnt, some more rapidly than others. This burning, though carried on in a peculiar manner, and though it never gives rise to a flame, yet produces an amount of heat which is as efficient as a fire to raise the temperature of the blood to 37° C. (98.6° F.).[1] The hot fluid constantly circulating in all parts warms the body like a house is warmed by a hot water apparatus.

Not only is the heat of the body produced by this constant oxidation of the living tissues, but this heat supplies the energy which has to be spent to produce the various movements taking place in the different limbs and organs. Exactly as the burning of coal in the furnace of an engine supplies the motive power which drives the flywheel and the various mechanical devices connected with it, in the same way the oxidation (or burning) of the muscles and ultimately of the food products, supplies the motive power which is necessary to carry out the movements of the body.

The various processes we have briefly sketched, namely, the alimentary, the circulatory, the excretory and the respiratory or oxidational processes, would be more than useless if they were not kept in strict proportion to one another.

If the state of physiological balance is to be maintained, not only must the quantity of food taken be at least

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[1] In the greater part of this work temperatures are expressed in terms of the Centigrade scale. That is, the temperature denoted by 0° is that of melting ice and the temperature denoted by 100° is that of water boiling at the normal atmospheric pressure and at sea level. When the zero and the 100° points are marked on the scale of a thermometer, the interval is divided into 100 equal parts or degrees, and the graduation is continued below 0° and above 100°. Temperatures below 0° are denoted by the sign —; those above by the sign +: thus —10° means a temperature 10° below zero, i.e., below the temperature at which ice melts.

In England the usual scale of a thermometer is graduated according to the Fahrenheit method, in which the melting point of ice is recorded as 32° and the temperature of boiling water is 212°. The space between the two is divided into 180 equal parts and the graduation extended below 32° and above 212°. To distinguish whether a given temperature is recorded in the Centigrade or the Fahrenheit scale, the letter C is added to the first, the letter F to the second. Thus 0°C is 32°F and 100°C is 212°F. The rule for the conversion of temperatures expressed in one of the two scales into the other is quite simple and is represented by the formula $F = \frac{9}{5}C + 32$ or its equivalent $C = \frac{5}{9}(F - 32)$. Thus, if we are given a temperature of 10°C the equivalent in Fahrenheit is $F = \frac{9 \times 10}{5} + 32 = 50°$. In other words, 10°C = 50°F. Likewise, if we wish to know how many degrees in Centigrade scale correspond to 50° in Fahrenheit, we find it from $C = \frac{5}{9}(F - 32)$ in which $F = 50°$. Therefore the Centigrade temperature will be $\frac{5 \times 18}{9} = 10°$.

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equivalent to the quantity of matter excreted, but the nutritious matter must be distributed with due rapidity to the seat of each local waste. The circulatory system is the commissariat of the physiological army. Again, if the body is to be kept at a tolerably even temperature, though that of the surrounding atmosphere varies, the condition of the hot water apparatus must be regulated.

In other words, a co-ordinating arrangement or system must be added to the above organs. This co-ordinating mechanism is the nervous system.

It is owing to the nervous system that we are aware of the need for food, that we discriminate nutritive from non-nutritive food. It governs the movements of the jaws and of the alimentary canal and determines the due supply of the juices necessary for digestion. It is the nervous system which supervises the movement of the heart and regulates the calibre of the blood vessels. It also governs the excretory and oxidational processes, and thus indirectly contributes to the maintenance of the hot water apparatus.

All the phenomena of nutrition generally are under the control (automatic) of the nervous system. Beside this automatic regulation, the nervous system presides to voluntary movement, and is also the seat of intellectual functions, as we shall see presently.

Though the bones of the skeleton are all strongly connected by ligaments and cartilages, yet the joints play so freely, and the centre of gravity of the erect body is so high that it is impossible to make a skeleton or a dead body support itself in the upright position. That position, easy as it appears, is the result of the contraction of a great number of muscles which oppose and balance one another. Thus, the foot forming the surface of support, the muscles of the calf must contract or the body would fall forward. This action would tend to bend the leg, but this is neutralised and the leg is kept straight by the muscles of the thigh. This action again would bend the body forwards, and this is avoided by the action of the muscles of the back. Thus, the erect position we so easily assume is the result of the combined action of a number of muscles. What is it which makes them work together?

Let any person in an erect position receive a violent blow on the head. He falls prostrate in a heap, his limbs relaxed and powerless. What has happened? The blow does not touch any muscle of the body, and in the greater number of cases, not a drop of blood is spilled. Indeed, if the "concussion" has not been too severe, the sufferer comes to himself again, and will soon be as well as ever.

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Therefore, no permanent injury has been done to any part, least of all to the muscles, but an influence has been exerted upon a something that governs the muscles. A similar influence may be the effect of various causes; a strong emotion or a bad smell has the same effect on some people as a blow.

This might lead to the conclusion that the mind governs the muscles. It is not so. There are many instances recorded of people who have been shot or stabbed in such a way that the spinal cord is wounded and partly severed. These people lose the power of standing though their mind is quite clear. Moreover, they do not retain any power of sensibility, i.e., of feeling what is going on, in their legs and likewise they lose the power of moving them at will. Yet, though the mind is cut off from the lower limbs, a controlling power over them is left. If the soles of the feet are tickled the legs kick. Again, if electric shocks are sent in the spinal cord, the limbs move even more powerfully than they do normally under the action of the will. Finally, if the cord is not merely severed but destroyed altogether, all the above phenomena cease; tickling or galvanic shocks have no effect, and the limbs connected with the part of the spinal cord that is destroyed lose all sensibility and power of movement.

Examination of this kind carried farther proves, as we shall see later, that though the brain is the seat of all sensations and mental actions, and the primary source of voluntary movement, the spinal cord by itself is capable of receiving impressions from the exterior and converting them not only into a simple muscular contraction but into a combination of such actions.

Thus, we can conclude that the nervous system, or more exactly, the cerebro-spinal nervous centres, have the power, when they receive certain impressions from without, of giving rise to simple or combined muscular contractions.

Now, the impressions we receive from without are of different characters. Any part of the surface of the body may be so affected as to give rise to sensations of contact and pressure, or of heat or cold, and any or every substance can, under certain circumstances, produce these sensations.

On the other hand, only a very few portions of the bodily framework are competent to be affected in such a way as to cause sensations of taste, or smell, of sight or of hearing, and only a few substances, or particular kinds of vibrations, are able to affect these parts. These limited parts of the body which put us in relation with particular forms of substance or with particular vibrations or forms of force, are

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termed the sensory organs. There are two such organs for sight, two for hearing, two for smell, and one for taste.

The work of nutrition generally is, as we have repeatedly pointed out, performed according to the laws of conservation of matter and conservation of energy. When we try to apply the physical and chemical laws to the nervous system we meet with what seems at first an insuperable difficulty.

It is true that mental and other nervous phenomena have been studied for a long time, but this study has been simply the study of these phenomena by themselves without a thought to their correlation with other phenomena of nature. It is a matter of quite recent conception that nervous phenomena have a direct relation to the other realms of nature. We shall revert to the subject in one of the next chapters.

**Brief Description of the General Arrangement of the Body.**

As we have already pointed out, the human body is evidently separable into head, trunk and limbs. In the head, the skull or brain case is easily distinguishable from the face. The trunk is divided into two parts, an upper one, the cavity of the chest or thorax, and a lower one, the abdomen; the separation of these two parts is effected by a muscular membrane, the diaphragm, the contraction and relaxation of which serves to increase and to decrease alternately the size of the upper cavity or thorax. Of the limbs there are two pairs, the upper one, or arms, and the lower one, or legs. Legs and arms are sub-divided by their joints into parts which exhibit a rough correspondence, or, as usually termed, an homology; the thigh corresponds to the upper arm, the leg to the forearm, the ankle or joint connecting the leg and the foot to the wrist or joint connecting the forearm and the hand. The bony framework of the hand corresponds to that of the foot and the fingers to the toes.

The whole body, apart from the viscera, i.e., the internal organs located within the thorax and the abdomen, is seen to be laterally symmetrical. That is to say, if it were split lengthways by a big knife passing along the middle line of both the dorsal and the ventral (or back and front) aspects, the two halves would almost resemble each other. One half of the body thus divided would show in the trunk the cut surfaces of thirty-three bones superimposed to each other with the interposition of very strong discs of tough substance, and joined together by ligaments so as to form a long column, the vertebral column, which lies much nearer the dorsal, or back, than the ventral or front aspect. As we shall see more precisely a little later, the bones thus cut through are the vertebræ. Each vertebra has a more or less

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circular opening, and the collection of these openings when the vertebræ are placed above one another as is the case in the living body, forms a long, narrow canal termed the spinal canal. This canal, which is occupied by a long whitish cord of nervous matter called the spinal cord, a most important part of the nervous system, is on the dorsal side of the vertebral column.

We have said just now that the trunk is divided into two main cavities, namely, the chest or thorax, and the abdomen, which are separated by a partition in the form of a fleshy muscular membrane called the diaphragm.

The thorax contains the lungs and the heart, while the abdomen receives the various parts of the alimentary canal, together with those organs (the kidneys) serving to the excretion of some of the waste products previously referred to.

Where the body is succeeded by the head, the uppermost part of the vertebral column is continued upwards by a continuous mass of bones which extends to the whole length of the head, and forms a double bony chamber; the back one is the cavity of the skull and contains a mass of nervous matter, the brain, which is continuous with the spinal cord; the front chamber or cavity of the face is almost entirely occupied by the mouth and pharynx, the latter being the upper end of the alimentary canal; the two orbital cavities also occurring in the front portion of the skull serve to lodge the eyes and their appendages, as we shall see presently.

The brain and the spinal cord together constitute what is termed the cerebro-spinal axis or cerebro-spinal centres, or again, the central nervous system. Thus a longitudinal section shows that the human body is a double tube, the two tubes being separated by the spinal or vertebral column, and the bony axis of the skull which forms the floor of the one tube and the roof of the other. The dorsal tube contains the cerebro-spinal centres, i.e., the spinal cord and the brain, the ventral one, the alimentary canal, the heart, the lungs, etc.

Transversal sections taken at right angles to the axis of the vertebral column or to that of the skull, show still more clearly the fundamental structure of the body, and explain that the difference in size of the head and trunk is due to the different size of the dorsal cavity relatively to the ventral one. In the head the former (the skull cavity) is large in proportion to the latter (the cavity of the face) whereas in the thorax and abdomen the dorsal cavity is very small.

The limbs contain no such chambers, but with the exception of certain branching tubes filled with fluids (the blood vessels and the lymphatic vessels to which we shall revert later on) they are solid or semi-solid throughout.

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## CHAPTER II.

### ANATOMICAL ELEMENTS. LIVING TISSUES. CONNECTIVE TISSUE.

**Anatomical Elements.**

The branch of science concerned with the general arrangement of the parts of the body referred to in the previous chapter constitutes what is called descriptive anatomy.

A further and more elaborate examination of the different parts and organs shows that these are made of different kinds of materials such as muscle (or flesh), cartilage or gristle, bone, fat, nervous matter, etc. These various constituents, entering into the structure of the various parts or organs, in the same way as bricks, wood, stone, etc., enter in the constitution of a house, are termed tissues. Some organs are made of one tissue only, others of several tissues. The study of these tissues, or fundamental structures entering into the constitution of the body, is termed Histology and has been created by the French scientist Bichat.

Though a certain amount of knowledge concerning the living tissues can be derived from observation with the naked eye, yet the microscope is absolutely necessary to arrive at definite conclusions on the subject of Histology.

The microscope shows that the various tissues whether hard, like bone, or firm, like flesh, or even jelly-like, are formed by the juxtaposition of extremely small particles called anatomical elements. Some of these elements have about equal dimensions in all directions and are termed cells. In others, the length is in excess of the other dimensions; such elements are called fibres. We shall presently study the muscular fibre, the nervous fibre, etc.

The size of living cells is always microscopic, the various cells of the human body being between 1/1,000 mm. and 1/10 mm. A fibre, which, as we shall see, is but an elongated cell, may be comparatively long, but its width is always microscopic.

Thus our body is made of an agglomeration of an almost infinite number of these small anatomical elements. It is in these elements that the phenomena of waste and of reparation which constitute life take place. When we speak of the nutrition of a human being we must think not of the big organic masses (limbs or organs) but of the microscopic elements (cells or fibres) which lie side by side and which

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work harmoniously and in common to maintain the life of the individual as a whole. All these cells and fibres are comparable to as many small beings which live independently from each other and whose total vital activities constitute the life of the individual.

Facts of observation support these views. There are small low animals, hydra, for instance, which can be cut up with impunity: each bit continues to live, and finally each one reproduces a whole hydra. Similar facts occur in animals nearer to man. The eye of a salamander or a triton can be reproduced after removal, as we shall see later on.

In man himself (and the same applies to all living beings) the independence of the anatomical elements has been proved by an experiment performed by a French surgeon, Garengeot, in the early part of the 19th century. A man had his nose cut off in a street brawl. He picked it up from the muddy ground and brought it to Garengeot, who cleaned the severed organ and fixed it in its normal position by the help of a few stitches. He found, to his surprise and delight, that the nose thus grafted in its position took root, and after a time assumed its original appearance. Since then, many instances have been recorded of noses or even fingers which have been replaced after being separated from the rest of the body, and have resumed their usual appearance and function.

Later on, Paul Bert removed the tail of a young rat for a length of two or three centimetres. He kept it for a few hours at a favourable temperature and then did not attempt to replace it in its position, but grafted it on the back of the animal. He found that the grafted tail took root at the place it was fixed, and grew to the normal length of 8 to 10 centimetres.

Hence it is correct to say that each part of the body has its individual life, and by part we do not understand each limb or each organ, but the anatomical elements (cells and fibres) whose collection constitute the various organs and generally the whole body itself.

Thus we arrive at the conclusion that the body has to be regarded as a collection of millions of anatomical elements, cells or fibres, grouped in various tissues, each of these elements being alive and working in harmony with the others to maintain the life of the body as a whole.

In this community, the constituent elements do not live in an isolated way. Each of them works for itself to be sure, but each also works for the good of the community, and depends on resources derived from other elements. Thus,

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in the above experiment performed by Paul Bert, the tail of the rat continued to live when cut off because it had stored a certain amount of foodstuff. When this is exhausted, the tail would die and could not resume life when grafted. If grafted while still alive, it will still receive (though in an abnormal way) the nutriment it requires. The blood itself, which, as we have pointed out, is the carrier of foodstuff, is manufactured and kept up by other anatomical elements. Thus everything is connected and in harmony in a living body in normal health, the integrity of the whole depending on the regular life of the constituent anatomical elements.

The modern conception of a cell and the doctrine that "the body of all animals and plants consists either of a single cell or of a number of cells and their products," and that all cells proceed from pre-existing cells, is the present basis of Physiology.

A single cell is a minute corpuscle of living substance or protoplasm, the size of which varies from 1/1,000 to 1/10 mm.[1] A cell is made of two distinct parts, the main substance or protoplasm in which a nucleus is embedded. The protoplasm often includes granules of nutritive material or of matter stored up for nutrition purposes. The external layer of the protoplasm is often altered so as to form a distinct cell wall, but this is more common in vegetal than in animal cells. This wall may be regarded as a thickening of the external protoplasmic layer, and its presence or absence is of small importance. The nucleus, on the other hand, is a most important part and presides to the nutritive activity and to the reproduction of the cell. It is regarded as the conveyer of hereditary characteristics. The protoplasm is a semi-fluid, transparent substance which swells up in water but does not dissolve in it, and does not mix with it. It consists of about 80 to 83 per cent. of water with 20 or 17 per cent. of solids, chiefly proteid or albuminoid matter. In fact, it is difficult to give an exact definition of protoplasm. The notion of protoplasm is inseparable from that of life, and up to now it has been found impossible to give a satisfactory definition of life. All we can say is that the term protoplasm applies to

[1] For the reckoning of the size of small objects only visible under the microscope the millimetre, the smallest unit generally used for measurement purposes, is considerably too large. It has been found convenient to use a special unit termed the micron, which is equal to 1/10000th of a millimetre and is usually denoted by the Greek letter $\mu$. Thus, a cell the size of which is 1/1000 mm. is said to be 1 micron; a cell of 1/10th of a millimetre is 100 microns and so on. In the chapter devoted to microscopic work, we shall explain how the size of a minute object seen under the microscope can be estimated.

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substances which, in circumstances necessary for the existence of living beings, exhibit vital manifestations which we will examine presently, and which consist mainly of assimilation and dissimilation, growth, reproduction and production of movement or of heat. As Claude Bernard puts it, protoplasm is the agent of the vital manifestations of the living cell; Huxley defines it as the physical basis of life.

The notion of protoplasm is therefore an abstract and general idea, like that of life itself, and does not correspond to a well-determined substance. There are an infinity of protoplasms, as many as there are living species, as many as there are distinct individuals in a specie, and as many as there are different cells in a given individual. It is true that the various protoplasms cannot be differentiated from the morphological standpoint, or from the standpoint of their physical or chemical properties, but they differ by their physiological reactions, and by the properties of the products they elaborate. The various hæmoglobins (or hemoglobins) which can be extracted from the blood are compounds of hæmatin (or hematin) and albumin.[1] Now the hematin is the same in all animals, and it is united to the same amount of albuminoid substance. Yet the hemoglobins derived from the blood of various animals crystallise in different ways. The hemoglobin of the human blood crystallises in long and narrow prisms; that of the cobaye (guinea-pig) in tetrahedrons; that of the squirrel in hexagonal plates; that of the turkey in cubes; that of the goose in fine needles arranged in the shape of a rosette, etc. These facts lead us to admit that the differences between the various hemoglobins are due to a different constitution of the albuminoid substance in different animals.

In a similar way the starch extracted from vegetal cells answers to the chemical composition represented by the formula $C_6H_{10}O_5$, but it presents itself in the form of grains of different size and appearance, according as it derives from different vegetals. When heated in water, the grains swell and give rise to a viscous and transparent liquid, and the temperature at which the swelling begins is variable; with the starch derived from the potato this swelling occurs when

[1] The word hæmoglobin, like many other words concerned with the blood, should be spelt with a diphthong since they are formed from the Greek prefix hæmo signifying "pertaining to the blood." Thus we should write hæmoglobin (to denote the colouring matter of the red blood corpuscles); hæmatin (to denote the product of decomposition of hæmoglobin); hæmorrhage (to denote an escape of blood from the blood vessels, either by diapedesis through intact walls or by rupture of the walls of the vessels), etc. These words are, however, frequently spelt hemoglobin, hematin, hemorrhage, etc.

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the temperature reaches 65° C., with the starch derived from corn the temperature of swelling is 70° C., with that obtained from rice it is 80° C.

The various kinds of starch are also acted upon more or less energetically by different reagents; they all become blue in the presence of iodine, but the intensity of the blue coloration is not the same for all, every other thing being identical. Thus, grains of starch, though having the same chemical composition, differ in their physical and chemical properties according to the various protoplasms from which they are elaborated. Similarly the fats which accumulate in the adipose cells of various mammals show wide variations in their point of fusion, according to the species from which they derive.

The way in which different living beings react in the presence of a same physical or chemical reagent shows also that the living substance of these beings, though apparently identical, must really differ very widely. This is proved by the more or less resistance of unicellular beings to a high temperature or a similar resistance to various poisons in higher types of living organisms. Thus a goat can bear without any apparent ill effect a dose of morphine which would put to sleep a great number of men.

We have said that the bodies of all beings are made of either a single cell or of a collection of cells.

The study of the vital properties of protoplasm or of cells generally is easily studied in the amœba, a unicellular living being found in stagnant water and damp earth, or again in the white corpuscles of the blood, which are examples of cells retaining their simple primitive form in the body of a higher animal.

In every pond with weed, a careful search will produce many microscopic creatures (or amœbæ) which represent one of the least elaborate types of living animals known. It is merely a minute morsel of jelly-like substance (or protoplasm) which changes its shape constantly. It has no wall but, as it does not dissolve in water, it remains separate from it as would be the case for a bubble of oil floating in water.

Carefully examined under the microscope, an amœba is seen to consist of an irregular mass of protoplasm with a nucleus embedded in it, the protoplasm being usually granular in appearance. Its shape changes constantly, the amœba being able, so to speak, to move its contents from one end to the other: processes or pseudopodes are extended and retracted, and the animal, by means of these processes,

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can change its position. In fact, the amœba can flow about in any direction, altering its shape to an indefinite extent, and forming itself either in a long projection, as a tiny trickling stream, or swelling into a more or less spherical knob. In this way it slowly moves about without, as far as can be seen, any apparent purposes. As the protoplasm, the jelly-like substance of which it is made, is filled with fine particles or granulations, the flowing of the fluid creature and the extension and retraction of its pseudopodes can easily be followed under the microscope. (See fig. 1.)

Hence, the living cell constituting the amœba has the power of movement. A white corpuscle exhibits similar spontaneous movements consisting in constant changes of shape and progression of the whole cell. Such movements are called amœboid movements, and all living cells possess this power to a variable extent.

Beside the apparently spontaneous movements just described, the living cell can be excited or stimulated by the action of external agents called stimuli generally. Mechanical pressure, heat, electricity, chemical reagents, and foreign particles can act as stimuli. When a suitable stimulus is

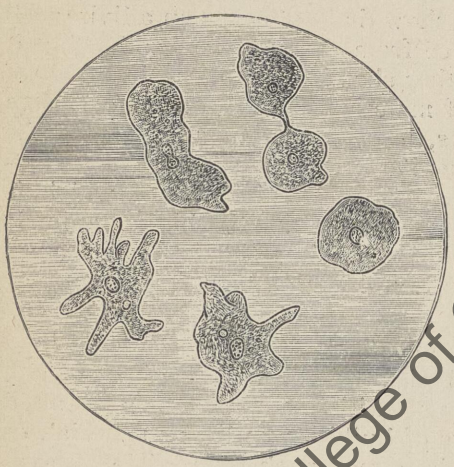

FIG. 1.

FIG. 1 shows the changes in shape of an amœba observed under the microscope with a magnification of about 500 diameters.

Similar changes may be observed in a white blood corpuscle. Note the production and the retraction of the protoplasmic process or pseudopodes.

applied to the cell, the latter exhibits its power of response by contraction of its mass, and changes in shape. This power of response to an external stimulation is termed Irritability. The so-called spontaneous movements we have referred to above are probably the effect of external stimuli.

If an amœba or a white blood corpuscle is carefully watched under the microscope it will be seen that when it comes across something suitable, some particle floating in the preparation, it begins to pour itself out in streams or

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pseudopodes which bend round the desired object. These streams, these pseudopodes, as they meet round the particle join together, and the object, the particle, is thus caught within the cell, and enters into the jelly-like protoplasm, where it gradually dissolves after undergoing chemical changes, and thus becomes incorporated in the protoplasmic mass of the cell from which it soon becomes indistinguishable. The part of the object that is not assimilated is rejected. This shows that the amœba feeds by literally putting itself outside its food. When the particle of food has been dissolved, the hard or insoluble or unassimilable portion of it is allowed to escape into the water, and the assimilated part goes to increase the size of the cell.

Thus, the living cell has the power of digestion and nutrition accompanied by a power of respiration. Exactly as in a living man oxygen is absorbed from the air, is drawn into chemical combination, and is afterwards rejected or exhaled, for the most part united with carbon in the form of carbonic acid gas, in the same way the power of assimilation of the living cell is accompanied by an absorption of oxygen and a rejection of carbonic acid gas.

Further observations show that not only can a living cell build up its own substance from the food it absorbs, but it may also be the seat of other chemical changes, the result of which is the formation of materials like glycogen (a variety of sugar), fat, or ferments, into its own substance. On the other hand, these constructive processes are always accompanied by destructive changes, the chief one of which is oxidation. We shall see presently that in higher animals special cells, in organs called secreting glands, are set apart for the production of ferments playing a most important part in the life of the animal.

The whole series of chemical changes occurring in a single cell and also in a body made of cells, beginning with assimilation and ending with excretion, is termed metabolism. The process of building up living material, or constructive metabolism, is termed anabolism. The process of breaking down materials into simpler products, or destructive metabolism, is termed katabolism.

Thus, the living cell exhibits a power of movement, a power of response to stimuli or irritability, a power of assimilation and growth.

When a single cell (e.g., an amœba or a white corpuscle) has reached a certain size, its power of reproduction comes into play. This power is manifested by a simple division of the cell substance, preceded by a division of the nucleus.

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Two cells, two amœbæ, or two white blood corpuscles, are thus produced, each of which will grow and ultimately divide into two other cells, and so on.

The problem of the origin of the living cell is one of the most difficult in biology, and we cannot discuss it in a work of this kind. For our present purpose it is sufficient to state that the researches of Tyndall, Pasteur, Lister, etc., have proved in a most definite way that "spontaneous generation" is an absolute impossibility, and that a living cell always originates from a pre-existing cell.

The body of man, and of every living animal, is developed from a single cell, the ovum or egg, which, after fertilisation, first divides into two, each of which divides again, and so on. After this process of division has proceeded for some time, the cells of the embryo become arranged into three layers, the outermost being termed the epiblast or ectoderm; the innermost is the hypoblast or endoderm, and the middle one the mesoblast or mesoderm. From these three embryological layers all the tissues and organs of the adult are formed.

In this process of development from the three embryological layers, there is no longer mere cell division, but the various cells become modified or metamorphosed from their original condition. Some become thin and flat, and, cohering at their edges, form blood-vessels. Others become elongated and thread-like to form the fibres of the muscular and the nervous tissues. Others become separated by intercellular substances derived from the cells themselves, and in this substance fibres such as occur in connective tissue or calcareous matter as in bone are deposited.

**Living Tissues.**

Having thus described the structure and properties of the protoplasmic units called cells, we must briefly study the different kinds of materials or tissues forming the various organs of the body. The number of distinct tissues in the human body may be reduced to five, namely:—

(*a*) The epithelial or surface-limiting tissue.
(*b*) The connective or supporting tissue.
(*c*) The muscular or contractile tissue.
(*d*) The nervous or sensory tissue.
(*e*) The blood and lymph or nutritive tissues.

Each kind may be sub-divided, but the various subdivisions are not always sharply defined, forms of transition being often recognisable.



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**Epithelial Tissue.**

An epithelial tissue or an epithelium is a tissue covering the external and internal free surface of the body, and is made of layers of cells placed side by side with a variable amount of cementing substance. It forms (1) the outer surface of the skin or epidermis; (2) the covering of mucous membranes, i.e., of membranes lining the passages and cavities communicating with the exterior and the ducts and tubes of glands opening in these cavities; (3) the terminal parts of the organs of special senses; (4) the inner surface of the serous membranes, i.e., those membranes formed of closed sacs which surround the viscera or internal organs of the body; (5) the inner surface of the heart, blood-vessels, and lymphatic vessels (Endothelium); (6) the inner surface of the cavities or ventricles of the brain and the central canal of the spinal cord.

Epithelial cells, like all living cells, consist mainly of protoplasm and a nucleus; having different functions (protective, secreting, etc.) and being exposed to various conditions, these cells present great variations of structure and form, some of which we shall investigate presently. As regards arrangement, epithelial cells may be stratified, i.e., forming several superimposed layers, or simple, i.e., arranged in a single layer. As regards shape, epithelial cells may be classified into squamous or flat, columnar or cylindrical, or cubical.

No blood-vessels pass into the epithelial tissues, the cells deriving their nourishment by imbibition of the plasma exuded into the subjacent tissues, but in many parts fine nerve fibres exist in the form of fine filaments distributed amongst the epithelial cells.

A peculiar form of epithelium is the ciliated epithelium, in which the cells, usually columnar, have at their free ends fine hair-like processes or cilia. Each cell has a brush of cilia 1/100 mm. long in the windpipe. These cilia exhibit during life and for a short time after removal, rapid whip-like movement. Each cilium bends swiftly in one direction, and returns to the upright position, in the fluid which constantly bathes the ciliated surface. It is thus that mucus is moved along the bronchial tubes and windpipe. Such ciliated epithelia are found in the respiratory passages, the ventricles of the brain, the canal of the spinal cord, etc. As we shall see at a later stage, the cause of the movements of the cilia in a ciliated epithelium is not entirely known; the source of motion is contained in the cell itself and is independent of any connection with nerve fibres.

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Various forms of epithelial cells are connected with the termination of certain sensory nerves to form a receptive end-organ for different kinds of vibrations (rods and cones in the eye; auditory cells in the ear, etc.). Such epithelia are called sensory.

Leaving aside the varieties of sensory epithelium we shall study later on, the main functions of an epithelium are either protective or secretive. The layers of epithelium covering the skin (epidermis), and that lining the air passages, the lids, etc., are mainly protective coverings. The epithelial cells of the salivary glands, of the gastric glands, of the liver, etc., are composed of protoplasm, which is the seat of active chemical operations, and in which new substances are formed from the blood and poured out as secretion to fulfil important functions, or again, are discharged from the body as excretions.

A ciliated epithelium is protective since it aids in propelling fluids and minute particles from the body.

**Connective Tissue.**

The term Connective Tissue applies to tissues apparently very different, but which perform a common function, that of binding and supporting the other tissues and organs or parts of organs of the body. The connective tissue is comparable to a certain extent to the cotton-wool filling a case in which fragile objects are packed; the objects themselves represent the different organs or the parts of a same organ.

It is a kind of connective tissue which forms an internal lining, more or less thick, to some epithelia in order to increase their resisting power.

Thus, the skin covering the human body is made of two parts, namely, a superficial part or epidermis, in the form of a stratified epithelium and a deeper portion termed the dermis, made of connective tissue. The epidermis is deprived of blood-vessels and of nerves, and can be cut off, as in shaving, without bleeding, and without any painful sensation. The dermis, on the other hand, is a sanguine structure which bleeds freely when cut, and is supplied with numerous nerve fibres, which explain its exquisite sensibility when the covering epithelium is removed. It is the dermis which tans when the skin is made into leather.

Another variety of connective tissue is the loose tissue which binds the skin to the subjacent parts. If one skins a rabbit, one can see that the skin proper is connected with the subjacent parts by numerous whitish filaments, the interlacing of which forms a loose network; this loose network

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is made of connective tissue, and forms a part of the great connecting medium by which the various parts and organs of the body are held together. It passes from the dermis of the skin between all organs, enclosing the muscles, coating the bones, etc. So completely does the connective tissue permeate almost all parts that if every other tissue were dissected away, a complete model or mould of all the parts and organs would be left consisting of this tissue.

We have mentioned before the mucous membranes, the soft reddish membranes which line the internal passages and cavities of the body which are in direct communication with the exterior and are continuous with the skin at the various orifices on the surface of the body. As an instance, we may mention the mucous membrane lining the mouth, the cavities of the nose and the air passages generally; another instance is the conjunctiva which lines the internal surface of the lids and the anterior portion of the eyeball.

A mucous membrane has a structure resembling that of the skin, i.e., it consists of a superficial layer or epithelium supported by a corium of connective tissue which is richly supplied with blood-vessels and nerves. In some regions, the mucous membrane is loosely attached to the subjacent parts by an areolar tissue similar to that connecting the skin and the organs beneath; in other regions, the mucous membrane is closely connected to the tissue beneath it (as in the tongue) or to cartilages (as in the larynx) or to bones (as in the nasal cavities).

In fact, a mucous membrane might be likened to an internal skin, only while in the true skin the outside epithelium becomes harder and more corneous (at least, in some parts) owing to atmospheric effects or to continued mechanical pressure, the epithelial surface of a mucous membrane remains soft and more or less velvety because it is kept wet by the fluid secreted by the glands of the subjacent portion, as we shall see presently. Besides, the epithelium of a mucous membrane is always comparatively thin, so that the blood circulating in the deep corium gives it its reddish tint.

The term "mucous membrane" is derived from the fact that the glands contained in the corium constantly secrete a viscid fluid or mucus which is poured on the epithelial surface.

As stated before, connective tissue varies very much in character, in some parts being soft and tender as is the case in the type of tissue binding the skin to the subjacent parts (a type which is termed subcutaneous owing to its location or areolar because of its mesh-work arrangement) sometimes more or less elastic (as in cartilage), sometimes very hard as in

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bone, which is but a variety of connective tissue. All connective tissues derive from the mesodermic layer of the embryo.

It is interesting to examine briefly the formation of connective tissue from the mesoderm of the embryo. Where such a tissue will ultimately be, there are at first only embryonic cells, all similar to each other, and closely packed together. When the process of formation of connective tissue begins, these cells separate from each other and assume the shape of a star with processes by which they remain joined together. At the same time, their protoplasm elaborates a peculiar albuminoid substance which flows from the cell body and occupies the intercellular spaces; for this reason, this substance is termed interstitial substance. In a general way, this term applies to any substance of cellular origin which ultimately condenses outside the cells which have formed it.

The interstitial substance of the connective tissue, instead of remaining homogeneous or amorphous (i.e., structureless) assumes gradually the form of filaments, which are of two kinds: (a) some are very fine, yellowish, elastic, ramified and undulated; they are called elastic fibres and are not destroyed by a 40 per cent. solution of potash. Such fibres are found in the walls of the arteries and in tendons, to which they give a certain degree of elasticity; (b) another part of the interstitial substance takes the form of larger and whiter filaments narrowed at intervals and longitudinally striated; they are the true connective fibres which are dissolved in a 40 per cent. solution of potash.

It should be borne in mind that the elastic and the connective fibres are not elongated cells (as is the case for nervous and muscular fibres, as we shall see presently), but are derived from products elaborated by the cell protoplasm which escape the cells of origin and assume the shape of filaments. These filaments are irregularly interlaced in the spaces left between the star-shaped cells, the whole forming a mesh-work, the interstices of which are filled with some of the interstitial substance which remains in its original amorphous state and constitutes what is termed the matrix.

Thus, connective tissue is made of three main elements, namely, star-shaped cells connected by their processes, elastic and connective fibres, cells and fibres being embedded in a variable amount of matrix or amorphous interstitial substance derived from the cells. It is frequently observed however, that amœboid cells travel in the meshes of the network; these cells are merely white blood corpuscles which have passed through the walls of the capillary blood-vessels permeating the tissue.

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For the purpose of description, we can classify connective tissue into:—(i.) **connective tissue proper**; (ii.) **fibrous connective tissue**; **and** (iii.) **bone.**

(i.) The connective tissue proper is represented by the dermis of the skin and the tissue which springs from the dermis and extends between the various organs or parts of organs, as we have mentioned above.

A special form of true connective tissue is the adipose tissue, in which the protoplasm of the cells becomes replaced by droplets of fat which ultimately fill the whole cellular cavity, the protoplasm itself being reduced to a very thin membrane and the nucleus rejected to the periphery or even disappearing altogether. This phenomenon especially occurs in the connective tissue forming the dermis of the skin, and the resulting tissue is termed an adipose tissue. When a fragment of adipose tissue is heated, the cells burst to enable the fat to escape in liquid form, and all that is left is a residue made of the cellular envelopes and the interlacing fibres together with the amorphous intercellular substance which may be present.

(ii.) The second variety of connective tissue may be subdivided into **white fibrous tissue and yellow elastic tissue.** The former, in which the white connective fibres we have alluded to just now are abundant, constitutes the chief part of the tendons of the muscles, whereas the latter, in which elastic fibres occur in predominating numbers, is present in the walls of the windpipe and that of the larger arteries; the elasticity of the constituting fibres serves to keep the vessels open.

In the white fibrous tissue, the connective fibres often arrange themselves in parallel bundles forming compact bands or cords termed ligaments (serving to connect the bones at the joints) and tendons (serving to attach a muscle to a bone). However, the tissue may also occur in the form of fibrous membranes, as is the case in the periosteum or external covering of the bones, the dura-mater or external coat of the brain, the aponeuroses enveloping and binding together various muscles, etc. In those cases, as also in the dermis of the skin and the corium of the mucous membranes, the bundles of interlacing white fibres form a more or less close felt-work. Compact white fibrous tissue, whether in the form of elongated bands or of fibrous membranes, has a shining pearly aspect; it is very strong and pliant and inelastic, while a certain amount of elasticity is the main character of the yellow elastic tissue.

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The term **cartilage** or gristle applies to a special variety of connective tissue occurring in the form of a tough bluish-white substance, opaque in mass but translucent when cut in thin slices. Though of firm consistence it is very elastic, yielding to pressure or torsion, but recovering its shape when the constraining force is removed. No nerves are found in cartilage, which is therefore devoid of sensibility. It is also non-vascular, and derives its nutriment by imbibition of the lymph which exudes from the capillary vessels of the surrounding tissues. Under the microscope cartilage is seen to consist, like all connective tissues, of nucleated cells immersed in a ground substance or matrix quite amorphous or homogeneous (i.e., without any definite structure, and having the appearance of a mass of glass). The matrix is permeated by the two varieties of fibres we have mentioned in the preceding page.

Cartilage is found where great strength and a certain amount of rigidity are required. It assists in binding bones together, yet allowing some degree of movement (as in the case of the discs separating the vertebræ of the vertebral column). It acts as a buffer to deaden shocks, it reduces friction at the various joints or articulations and, in the form of costal or rib cartilage, it forms an important part of the framework of the thorax to the walls of which it imparts the necessary elasticity to allow the expansion of the lungs during respiration.

To sum up, the connective tissue differs from an epithelial tissue in a very essential feature. In an epithelium the constituting cells are placed close together, and though these cells may be and generally are united by a certain amount of interstitial substance this amount is always very small.

In any form of connective tissue, and especially in cartilage, a relatively considerable amount of intercellular or interstitial substance (the matrix) originates from the nucleated protoplasmic cells. Hence the cells are more or less embedded in a substance differing from them which constitutes the matrix. In an epithelium, though the cells may be joined together by a cement material, this is never abundant enough to deserve the name of matrix.

(iii.) **Bone.** With the exception of the enamel of the teeth, bone is the hardest structure of the body; yet it possesses considerable toughness and elasticity. In its fresh state, bone is pinkish white externally and reddish internally. On cutting through a bone, it is easy to see two kinds of bone tissue, a hard and compact tissue, like ivory, forming

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the outer shell and a looser tissue internally, with fibres and thin plates having the appearance of lattice work, called the cancellous tissue; a gradual transition from one to the other is often apparent.

In a long bone, like the femur (or thigh bone) or the tibia (one of the bones of the leg) the large round ends consist of the cancellous tissue with a thin coating of compact tissue.

A fresh or living bone is covered by an outer tough fibrous membrane called the **periosteum.** From a close network of blood-vessels in the periosteum, branches find their way through small openings on the surface of the bone, mainly to nourish the compact tissue; these vessels run in the bone through tiny channels called Haversian canals. By stripping the periosteum from the surface of a living bone, small bleeding points, indicating the entrance of the periosteal vessels, may be seen, and longitudinal sections of a long bone show not only that the substance of the bone is well supplied with blood, since this is seen to exude in all parts, but that the interior of the bone is occupied by a cylindrical cavity filled with marrow. Beside the blood derived from the periosteum, long bones have an artery which enters at some part of the shaft, passes into the medullary canals and breaks up in the marrow. Smaller vessels reach the articular extremities to supply the cancellous tissue; during life, the spaces of the cancellous tissue contain marrow and blood-vessels. Flat bones like the shoulder blade and short bones like those of the wrist or the ankle have no marrow internally, and are merely made of a central mass of spongious tissue surrounded by more compact tissue. There is always, however, a thin layer of marrow substance between the periosteum and the bone itself.

We cannot go into details with respect to the arrangement of the skeleton, i.e., the bony framework for the support of the soft tissues of the body; the skeleton includes various cavities for the reception of important organs as the brain, the spinal cord, the eye, the heart, the lungs, etc. Moreover, some of the bones of the skeleton act as levers for the action of the muscles and joints to aid in the locomotion of the body. We shall, however, describe at a later stage the portion of the skeleton constituting the orbital cavities and the surrounding parts.

Though bone is apparently rigid it has a certain degree of elasticity, as shown by the rebound of a skull dropped on the ground. Bone may be regarded as a form of connective tissue in which the interstitial substance has been

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replaced by mineral matter, mostly phosphate of calcium, carbonate of calcium, with a small proportion of calcium fluoride and magnesium salts. The hardness and compactness of bone depends upon the mineral matter it contains; its elasticity and toughness, upon the animal matter. The mineral matter may be removed by placing a bone in diluted hydrochloric acid: the bone will not be altered in shape but can be twisted and bent in any direction. In fact, bone from which the mineral matter is thus removed assumes the appearance of cartilage, and this by prolonged boiling in water will yield gelatine as all connective tissues do in the same circumstances.

On the other hand, the animal matter contained in bone can be removed by exposing the bone to red heat for some time in a closed vessel; nothing will be left but a mass of white bone-earth which has the general form of the bone but is very brittle and easily reduced to powder. The average relative proportion of mineral and animal matter in bone is 66.7 per cent. of the former, to 33.3 per cent. of the latter.

A point which is of importance in the study of the skeleton is the phenomenon termed **ossification.** Practically all bones are soft and flexible in the fœtus and in the young; they are really cartilages and not true bones, but they gradually harden and become converted into bones. This transformation is regular; every long bone like the femur or thigh bone or the humerus (bone of the upper arm) originally cartilaginous begins to become bone at three points, namely, at the middle and near each end. It follows that at a certain period of development there are really three distinct bones joined by the parts which are still cartilaginous. The epoch at which these points of ossification, as they are called, appear, and the moment when the three partial bones will be joined into one are well determined. In the human child these modifications have been studied so carefully that it is possible, by inspection of a skeleton, to tell the age of the child to whom it belonged. For instance, in the humerus, the joining of the inferior part with the middle one takes place at the age of 15 or 16, the junction of the middle and the superior part at about 20. This fact is of importance, since so long as the various parts of a given bone are not joined, they may increase in length by elongation of the soft intermediate parts between the points or centres of ossification. When the joining has finally occurred, a process which is generally completed at the age of 20 to 25, no increase in the length of the bone is possible.

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The bones in the skull present a somewhat similar phenomenon. In the young they are isolated, while later on they join together by a kind of an irregular dovetailing arrangement of extreme strength. It is easy to observe that in very young children there are, on the top of the head, two spots not protected by bones, and in which pulsation of the arteries of the brain can be seen or felt; these openings or fontanelles correspond to the parts where the bones will ultimately join, generally towards the end of the second year.

Another point of interest lies in the fact that the marrow is capable of reforming new bone tissue. Not only does the marrow fill the central canal of long bones, but in flat and small bones it also exists in the form of a thin layer, between the periosteum and the bone itself. If a little fragment of marrow taken from a young animal is introduced under the skin, even far apart from the bone from which it has been taken, it will be found after a time to have been converted into a real bone. Even if a whole bone is removed, care being taken that the surrounding periosteum, together with the thin layer of marrow attached to it be respected, this marrow will reform the bone. There are many instances recorded of children whose tibia has been removed, and who can walk almost without a limp on the new tibia the marrow has re-formed.

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## CHAPTER III.

### LIVING TISSUES—*(Continued)*. MUSCULAR TISSUE.

**Muscular Tissue.**

From the brief account we have given of the work of the body regarded as a machine, it should be quite clear that, owing to the law of conservation of energy, no work can be produced without the expenditure of an equivalent amount of energy. Exactly as the work done by a steam engine is derived from the energy stored up in the coal or the fuel which serves to transform the water of the boiler into steam under pressure, in the same way, the active power of the human organism, i.e., the capacity of the living body to produce mechanical work, is due to the energy set free by the oxidation of the food products. The organs which produce total or partial movement of the body are of three different kinds, namely, (i.) cells exhibiting what we have already alluded to under the heading of amœboid movements; (ii.) cilia; and (iii.) muscles.

We have already mentioned the amœboid movements of the white corpuscles, and it is probable that similar movements are performed by many other cells in various parts of the body. The amount of movement of which cells are capable is small, but, for all that, there are reasons for thinking that such amœboid movements are of great importance in the economy of the body, as we shall see presently.

The movements of the cilia in a ciliated epithelium are comparable to the amœboid movements just referred to. Each cilium may be regarded as one of the movable processes or pseudopodes of a white blood corpuscle, a ciliated cell differing from an amœboid cell in that its contractile processes are permanent, have a definite shape and are localised in a particular part of the cell, and that the movements of the processes, or cilia, are performed regularly and always in the same way. The movements of the cilia are not controlled by the nervous system, the required energy being evidently dependent on the life of the cell itself.

From our present point of view, the above structures are comparatively unimportant, since the greater part of the mechanical work of the body is mainly effected through the working of the muscular tissue. The muscles, generally using the bones as levers, are the agents which produce movements.

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**Chief Property of the Muscular Tissue.**

The special property of the muscular tissue is the power of contraction under an excitation or, as physiologists put it, under a stimulus. If a man extends his arm and the upper end of this limb is tightly grasped by another person, the latter will feel a great soft mass which swells, hardens, and becomes more prominent as the man bends his fore arm towards the upper arm. On dissecting the limb, the part which thus changes its configuration is found to be a mass of red flesh sheathed in connective tissue. The sheath is continued at each end into a tendon attached to the shoulder bone on one hand, and to the bones of the fore arm on the other. The mass of flesh is the muscle called biceps, and this muscle has, like all other muscles, the power of changing its dimensions, i.e., of shortening and becoming thick in proportion to its shortening, this power being exerted under the influence of the will, as well as under other causes termed stimuli. When the stimulus which has produced the above change ceases to act, the muscle returns to its original dimensions. This temporary change in the dimensions of a muscle, this shortening and thickening, is spoken of as "contraction": the return to the original dimension is termed "relaxation." It is owing to this property that muscular tissue becomes the great motor agent of the body.

**Various Kinds of Muscles.**

The various kinds of muscles may be conveniently divided into two groups, according to the manner in which they are fastened at their ends. The great majority of the muscles are, like the biceps (which has just been mentioned), attached at both ends to the solid levers formed by the bones. It may happen that the bone to which one end of the muscle is attached is absolutely or relatively stationary, while that to which the other end is attached is movable; in such cases, the attachment to the stationary bone is termed the origin, that to the movable bone, the insertion of the muscle. Thus, the origin of the biceps is on the shoulder bone, the insertion is on the bones of the fore arm, namely, the humerus and the ulna.

Some muscles are not attached to solid levers or bones. For instance, and as we shall see later on, the sphincter muscle of the iris is of circular shape, and is disposed in the stroma of the iris, round the aperture called the pupil. Contraction, i.e., shortening of this muscle, causes the pupillar aperture to decrease in size. In a similar way muscular tissue is found in the wall of the heart cavities or chambers, and the contraction of one of these muscles causes

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the corresponding chamber to become smaller, thus forcing the blood contained in it to flow through the blood-vessel opening in that chamber. In the alimentary canal, the blood-vessels and in many other parts, similar muscles occur, the purpose of which is to propel the contents of these parts in a definite direction. The ciliary muscle, i.e., the muscle serving to adapt the dioptric power of the eye to the distance of the object that is being looked at, belongs to the same class, as we shall see later on. Five out of the six extra-ocular muscles which we shall study in detail at a later stage, have their origin on the periosteum of the bones at the apex of the orbital cavity, and their insertions on the sclerotic coat. These muscles, together with the levator palpebræ superioris, which has its origin on the periosteum of the bones at the apex of the orbit and its insertion in the tarsal tissue of the upper lid, form, therefore, a transition between the two main kinds of muscles mentioned just now.

**Microscopic Structure of Muscles.**

On examining various muscles under the microscope we find that they all consist of elongated elements termed muscular fibres. In those muscles the contraction of which is not under the influence of the will, the muscular fibres appear distinctly as elongated cells, i.e., they consist of minute elongated, spindle-shaped threads in the central part of which a nucleus is seen. The average length of these fibres is 50 microns, their width 6 microns. The substance of the fibre is longitudinally but not transversally striated, and each fibre seems to have a delicate sheath. The fibres are collected together and united by a small quantity of cementing substance into bundles surrounded by connective tissue carrying nerves and blood-vessels. Each fibre is capable of contracting, i.e., of shortening, and becoming at the same time thicker.

In muscles the working of which is more or less under the control of the will, microscopic examination shows that they are also made of fibres bound up together in bundles surrounded by connective tissue carrying nerves and blood-vessels, but these fibres differ from those of the previous kind. If we examine a voluntary muscle like the biceps we find that it is contained in an external wrapping or perimysium, i.e., a sheet of connective tissue, from the inner surface of which partitions proceed and divide the space which it encloses into a great number of longitudinally arranged compartments; the muscular fibres themselves occupy these compartments, while the external sheath and the partitions proceeding from it carry the blood-vessels

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which thus surround the fibres without entering them, and also the motor nerves which at first lie in the sheath and the partitions but eventually enter the muscular fibres. The perymisium forms a complete envelope around the muscle; at each end it usually terminates in dense connective tissue or tendon which becomes continuous with the bone or the structure to which the muscle is attached.

As the sheath of a muscle and its partitions are made of connective tissue, they may be destroyed by prolonged boiling, in fact, in "meat boiled to rags," we have muscles which have been treated in this way; the perymisium and its partitions are broken up, and the muscular fibres, little attacked by boiling water, are readily separated from each other.

If a piece of muscle of a rabbit which has been boiled for several hours is placed in water and is teased out with needles, the muscular fibres are easily isolated. Under the microscope such a fibre is found to have a length of about 30 to 40 mms. and a width of about 60 microns. It is a cylindrical or polygonal rod with tapering or bevelled ends, by which it adheres to similar fibres or to the tendon terminating the muscle.

A living muscular fibre of the voluntary variety appears as a pale transparent rod composed of a soft, flexible substance, transversely striped as if the clear glassy substance were, at regular intervals, transformed into ground glass: hence the name of striated applied to this type of fibre.

Thus, the various muscles may be divided physiologically into two great classes: the voluntary or striped or striated muscles, the contraction of which is under the control of the will, and the involuntary or unstriped or smooth muscles, the working of which is not under the control of the will. The names of the two varieties are derived from the appearance of the fibres constituting the muscles. A voluntary fibre appears with an alternate dim and light cross striation, and looks, therefore, as if it were made of thin discs of clear glass and ground glass alternating with one another. An involuntary fibre does not show any such transversal striation, but appears as a spindle-shaped elongated cell, the surface of which is smooth, or, faintly striated in the longitudinal way.

As a rule, plain or smooth or involuntary muscles are never found to be attached to bones, but are associated with other tissues; such muscles occur in the walls of the alimentary canal, of the blood-vessels, etc. Striated or voluntary muscles are, on the other hand, attached to bones at least at one end. The only exception to the rule is

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observed in the case of the muscles found in the walls of the heart chambers. Such muscles, though not under the control of the will, belong to the striated or striped variety.

**The Chemistry of Muscle.**

From a fresh muscle cooled down to keep it from undergoing changes, and submitted to a great pressure, the contracted semi-fluid substance of the fibres can be squeezed out from the sheath of connective tissue, in the form of a viscid liquid termed muscle plasma, which remains liquid so long as it is adequately cooled, but which soon coagulates at ordinary temperatures, i.e., separates into a transparent muscle clot and a watery fluid or muscle serum. The muscle clot is mainly formed of proteid or nitrogenous substance termed myosin, and in the formation of myosin by the clotting of muscle-plasma, an acid termed sarcolactic acid is developed; the formation of this substance explains why the fluid, which, when first squeezed out was faintly alkaline, becomes distinctly acid.

A similar clotting takes place in the muscles of the body at a longer or shorter time after death. The muscles become gradually less elastic, and set into hard, rigid masses which retain the form they possessed when the clotting began. Hence the limbs become fixed in the position in which death found them, and the body passes into the condition termed "rigor mortis" or "death stiffening." At the same time the muscle, which was faintly alkaline or neutral in the living state, at least when at rest, becomes distinctly acid when rigor mortis sets in. It may be remarked that a similar though slighter acidity is developed in a living muscle when it contracts. A certain time after rigor mortis has set in, the coagulated matter liquifies and the muscles pass into a loose, flabby condition, which marks the beginning of putrefaction. Observation shows that the sooner rigor mortis sets in the sooner it is over, and the later it commences the longer it lasts. The greater the amount of muscular exertion and consequent exhaustion before death, the sooner rigor mortis sets in.

**The Mechanism of Muscular Contraction.**

By removing the muscle of the thigh (or gastrocnemius muscle) from a recently killed frog, whose tissues retain their vitality longer than those of a warm-blooded animal, the living muscular substance may be studied experimentally. The muscle is dissected out so as to be still attached to the femur or thigh bone and the sciatic nerve, which goes to the muscle, is isolated. Such a muscle with its attached

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nerve is called a muscle-nerve preparation. On stretching the muscle it is found to be extensible and elastic: its elasticity is slight but perfect, that is to say, a small force will extend it, but it returns exactly to its original length when the force is removed. The elongation of a muscle is not proportional to the force applied to it, but diminishes as the force increases. The most important property of a living muscle is its power of shortening when acted upon by a stimulus, its volume or bulk remaining the same. Normally, a muscle contracts in response to a stimulus from the central nervous system, but other kinds of stimuli may be applied; these may be mechanical (pricking or pinching), or chemical, or thermal, or electrical, and the stimulus may be applied to the nerve supplying the muscle or to the muscular tissue itself.

It should be observed that a healthy muscle, when at rest, is contracted to a small degree. This small amount of contraction, which is known as the tone of the muscle, is due to the influence of the nervous centres for, on cutting its nerve, the muscle becomes slightly longer. That the muscular fibres have in themselves the power of contraction is proved by the effect of a drug, called curare, which paralyses the motor nerves ending in muscles, whilst the muscular tissue still responds to direct stimulation.

To study the phenomenon of muscular contraction, the graphic method is convenient (see fig. 2). The muscle (M), prepared as stated above, is hung by one of its tendons, a string is attached to the other tendon and is made to pass round a light pulley. A small weight is fixed at the end of the string. It is clear that if the muscle shortens the pulley will turn in one direction, if it lengthens the pulley will turn in the opposite direction. In order that a small rotation of the pulley in one way or the other may be made apparent, a light pointer (A) is fixed to it. Let us assume that when the muscle is at rest the pointer is horizontal. As the muscle is no longer under the influence of the animal's will, an electric shock is used as stimulus instead of the nervous impulse which, in normal conditions, constitutes the stimulus acting upon the muscle. For this purpose, the wires of an electric battery (B) are connected with a needle (N) inserted in the muscle, and with the portion (S) of sciatic nerve which enters the muscle. A Morse key (K) is placed in the electric circuit in order that a current of practically instantaneous duration may be produced in it. When the circuit is closed for as short a time as possible, the following changes take place in the muscle: (a) the muscle becomes shorter and thicker, and therefore lifts the weight attached

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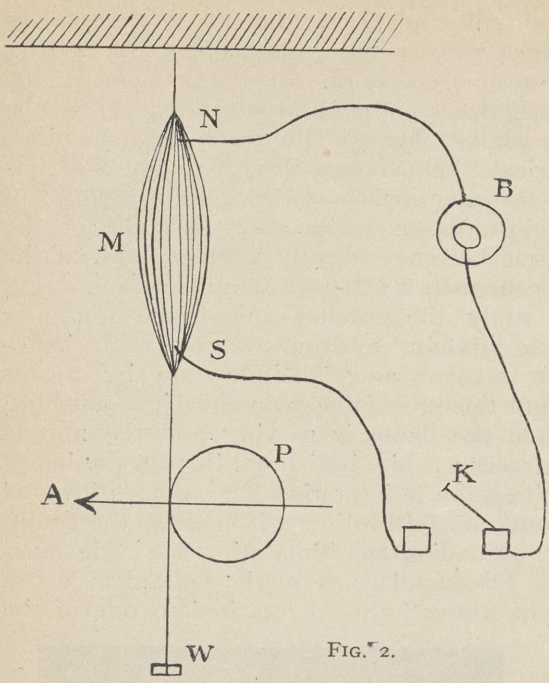


FIG. 2. MUSCLE-NERVE PREPARATION FOR THE STUDY OF THE MECHANISM OF A MUSCULAR CONTRACTION.

The gastrocnemius muscle (M) (i.e., the muscle of the thigh) of a frog, dissected away immediately after the animal is killed, is hung by a thread attached to its upper end; at the other end another fine thread is attached and carries a small weight (W). The lower thread is made to pass round a light pulley (P) at the centre of which a light pointer (A) is attached. The electric current generated by a cell (B) is made to pass through the muscle, the two ends of the conducting wire carrying needles (N) and (S) which are introduced into the substance of the muscle. Alternatively, and if the nerve (the sciatic nerve) which supplies the muscle has been preserved, the end (N) of the electric wire may be connected with it while the other end (S), fitted with a needle, is introduced in the muscle substance as stated before. An interrupting device, for instance a Morse key (K) serves to close or to open the electric circuit at will. Every time the circuit is closed or is opened again, the effect on the muscle, i.e., its contraction or shortening, is shown by a rotation of the end of the pointer (A). The return of the muscle to its normal state of rest is shown by the pointer resuming its original position.

The movements of the pointer (A) are recorded on a revolving drum covered by a sheet of paper coated with lamp black. To record short intervals of time a tuning fork, the vibrations of which are produced by an electrical device, has a fine platinum wire attached to the end of one prong. A given tuning fork when vibrating performs a definite and fixed number of vibrations per second, say 100 for the sake of argument, this number of vibrations corresponding to the pitch of the sound produced when the fork is excited. It follows that if the fine wire which vibrates with the prong to which it is attached is just touching the revolving drum, the oscillation will be recorded on the surface of the drum in the form of a regular wavy line, the intervals between a particular crest of this wavy line and the next one corresponding to the duration of a complete vibration of the fork and therefore representing an interval of time equal to 1/100th of a second in the case of the tuning fork we have mentioned. Should we use a tuning fork giving a sound corresponding to 200 or to 500 vibrations per second, we would have a graphic record of intervals of time equal to 1/200th and 1/500th of a second.

By a proper mechanical arrangement, it is possible to obtain on the same recording sheet the wavy line which represents intervals of time of 1/100th of a second, together with the curve drawn by the movements of the pointer (A) when the muscle contracts or relaxes. These curves are shown in FIG. 3.



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to it and causes the pulley to turn so that the pointer moves upwards. This effect is extremely brief, and is followed by the return to the normal condition which is shown by the pointer assuming again its horizontal position; (b) at the same time as the above changes are produced, chemical, calorific and electrical phenomena occur, carbonic acid gas is given off by a working muscle and a certain amount of sarcolactic acid is produced within the substance of the muscle. The muscle becomes slightly warmer, and, at the moment contraction begins, it acts as a small electric battery.

In order to study the mechanism of the muscular contraction more accurately, a drum covered with lamp-black is made to revolve at a definite rate by means of a clock-work, and the end of the pointer is just touching its surface. When the drum is moving and the muscle quiet, the pointer traces a white horizontal line on the lamp-black surface. When the pointer rises or becomes lowered again, its movements are faithfully registered on the drum.

We give (fig. 3) a diagram illustrating a single muscular contraction. The small curve at the bottom is traced by the vibrations of a small thread attached to one of the

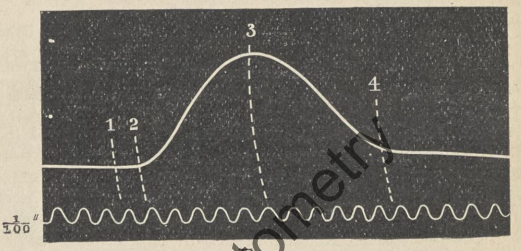


FIG. 3.

FIG. 3 (after Waller) is the diagram of the muscular contraction obtained by means of the apparatus shown in FIG. 2. The lower part of the figure represents the intervals of time recorded by a tuning fork vibrating at the rate of 100 oscillations per second.

The upper part is the graph of the muscular contraction itself. The point marked 1 on the curve corresponds to the exact moment the electric circuit is closed. It is seen from the diagram that the muscle does not begin to alter its length for a little while after the circuit is closed, the shortening of the muscle begins at the point marked 2, so that the latent period extends over a period of 1/100th of a second. The muscle then shortens and reaches the condition shown by 3 which corresponds to the maximum contraction; the interval between 2 and 3 reckoned on the lower or time curve thus amounts to 4/100ths and the interval between 3 and 4, i.e., the period of relaxation, is 5/100ths of a second.

prongs of a tuning fork, the rate of vibration of which is 100 per second. Therefore, each of the indentations of the curve corresponds to a single vibration and represents a period of time of 1/100th of a second.

An examination of the curve shows that the contraction consists of three phases: (1) a phase termed the latent period during which no apparent change takes place in the muscle. This interval represents the time necessary for the

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electrical impulse to be propagated along the nerve and for the preparatory change in the muscle itself. It becomes longer as the muscle is fatigued. (2) A phase of shortening or contraction during which the pointer rises. The height of contraction diminishes as the muscle tires, though the length of the period remains the same. (3) A phase of relaxation or return to the original length, during which the pointer falls into its normal position. This period becomes longer as the muscle tires.

The diagram shows that in the case of a fresh muscle the latent period occupies about 1/100th of a second, the phase of contraction 4/100ths, and the phase of relaxation 5/100ths. A single muscular twitch or a single muscular contraction is thus completed in about 10/100ths, or 1/10th of a second, but, as already stated, the time varies since, in a fatigued muscle, both the latent period and the period of relaxation are lengthened. These figures apply to a voluntary or striped muscle. As a rule, the contraction of a smooth or involuntary muscle is characterised by the fact that the latent period, i.e., the passage from the state of rest to the active state, takes a longer time (from 4/10ths to 8/10ths of a second) than in the case of a voluntary muscle. The period of contraction also lasts longer (sometimes several seconds) and the period of relaxation lasts even longer than the period of contraction. For this reason, voluntary muscles are often termed quick-acting, and involuntary, slow-acting muscles.

**Tetanic Contraction of Muscles.**

In the experiment described just now, it is evidently easy to stimulate a muscle twice in such rapid succession that the second stimulus is given while the muscle is still in the period of contraction resulting from the first. In this case, the muscle responds to the second stimulus as well as to the first; in other words, it contracts still more while already contracted. The second contraction takes place on top of the first, is rather less in amount than the first, and is added on to the first. If now a rapidly successive series of stimuli be applied, the muscle responds by an equally rapid series of contractions, each of which takes place before the preceding one is over. The whole series is thus added together and the muscle remains in a state of continued contraction as long as the stimuli are continued until exhaustion sets in. A prolonged contraction made up of such a series of single contractions super-added to each other, is called a tetanic contraction, and a muscle in this state is said to be in a condition of tetanus or cramp or spasm.

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Tetanus may occur as the result of disease (lockjaw), or may be produced by poisons like strychnine, or again it may result from overwork, as is the case in spasm of the ciliary muscle. A good instance of a clear case of tetanus is seen when a person takes hold of the handles of an induction coil in action. Cramp or tetanus is produced in the muscles of the fingers and the hands by the rapidly repeated contractions, and the subject cannot let go the handles until the current working the coil is cut off.

An exhausted or fatigued muscle cannot act owing to the accumulation of waste products, especially sarcolactic acid; if left to rest it may recover, the circulating blood bringing fresh nourishment and carrying off the accumulated waste products.

The voluntary contractions by which we perform the various movements of our body are in reality tetanic contractions, however short they may appear to be. Thus, when we contract one of our muscles by an effort of the will, it appears that a series of impulses is sent out in rapid succession from the nervous centres at the rate of twelve or more in a second, to throw the muscle into prolonged contraction. In this way, our control of the resulting movements is far greater than it would be if we were only able to execute a single, short and sudden contraction such as results from sending a single impulse along the nerve going to the muscle.

**Irritability of Muscles.**

To sum up, the power of contraction or irritability is the property of muscles to contract under the action of certain causes termed stimuli generally. Stimuli may be classified into mechanical stimuli (as pinching or pricking), thermal stimuli (application of heat causing a change of temperature), luminous stimuli due to the action of light, as we shall see more fully in dealing with the contraction of the pupil, electrical stimuli (due to the action of an electric current), and chemical stimuli (due to the action of some irritating substance). The natural stimulus of muscles is, however, in the greater number of cases, the nervous impulse originating in the brain centres and carried to the muscle by a nerve acting as a mere conductor of such impulses. This nervous impulse is often voluntary, but it generally acts on striated muscles with the exception of the muscles located in the walls of the heart. Smooth muscles act independently of the will, though under the control of the nervous system, as we shall see later on.

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We have pointed out that electric currents are used to study the mechanism of the muscular contraction. A direct current like that supplied by an ordinary battery determines a contraction immediately the circuit is closed, and again when it is opened, the muscle remaining at rest during the passage of the current.

With alternating currents of comparatively low frequency, or with direct currents interrupted at short intervals, the muscular contractions take place at such a quick rate that the muscle has no time to relax between two successive electric shocks; it remains permanently contracted, i.e., it assumes the state we have described as tetanus. This occurs when the frequency of the alternating current reaches a value of twenty-five to thirty alternations per second, or when the circuit of a direct current is alternately closed and opened at about the same rate. Industrial alternating currents of high voltage, with a frequency of about 100 per second, are generally fatal to human life because they cause a general tetanus of all muscles including those of the heart and those of the diaphragm. High frequency currents have different effects. Such currents are produced by the discharge of Leyden jars or by some similar device. The frequency may reach a degree of several millions per second, and such currents amount to electric vibrations comparable to light vibrations. A subject placed in a coil in which such currents travel does not experience any painful sensations, and shows no muscular contraction. Yet his muscles are set in a state of vibratory movement. D'Arsonval has found that muscles enter into contraction only if the frequency of the current is less than 5,000 per second.

High frequency currents have, however, a marked effect on the organism; they determine a superactivity of the oxidation of the tissue and of the intracellular nutrition. The amount of carbonic acid gas eliminated increases, the temperature of the body is raised and the subject experiences a loss of weight, accompanied by a greater production of urea and uric acid as a consequence of the greater waste of the tissues. At the same time, they determine an important dilation of the blood-vessels by direct action on the vasomotor nervous centres; the result is a diminution of as much as 5 or 6 cms. of mercury in the blood pressure. Such currents are now frequently used for the treatment of arteriosclerosis, an affection consisting in a hardening and consequent loss of elasticity of the walls of the arteries, which in its turn may lead to an arterial hypertension liable to produce cerebral hemorrhage.

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## CHAPTER IV.

### LIVING TISSUES—*(Continued)*. NERVOUS TISSUE. GENERAL ARRANGEMENT OF THE NERVOUS SYSTEM.

**Nervous Tissue.**

The nervous system, whose function is to guide, regulate, harmonise and co-ordinate the working of the various organs of the body, and also to preside to the perception of sensations or feelings and to the intellectual faculties, consists mainly of (a) masses of nervous matter situated in the bony cavity of the skull and in the central canal of the vertebral column, these masses forming what is called the nervous centres or the cerebro-spinal system; (b) cords of nervous matter or nerves, extending from the nervous centres to practically all parts of the body; (c) smaller masses of nervous matter termed ganglia which lie along the nerves situated in the neck, the thorax and the abdomen, and form the so-called sympathetic system.

The cerebro-spinal system consists of the portion of the nervous centres located in the skull, namely, the brain or encephalum, which is divided into the cerebrum or large brain and the cerebellum or small brain. The portion of the cerebro-spinal system lodged in the canal of the vertebral column is the spinal cord, which is united to the brain by the bulb or medulla oblongata.

The brain, together with the twelve pairs of nerves which emerge from it (cranial nerves) will be examined presently. Passing out from the spinal cord are thirty-one pairs of nerves, termed spinal nerves, which are distributed to all parts of the body, especially the muscles and the skin.

The sympathetic system consists, in the main, of a double chain of small swellings or ganglia, on each side of the front of the vertebral column, connected with each other and with the spinal nerves. Cords, termed sympathetic nerves, pass from these ganglia to the viscera (i.e., to the internal organs), to various glands, and to the walls of the blood vessels. These nerves on their way to the viscera sometimes unite with each other to form interlacing networks or plexuses, on many of which collateral ganglia are found. (The term Viscera is the plural of Viscus, a Latin word denoting any one of the organs contained within one of the three great cavities of the body, the cranium, the thorax, and the abdomen.)

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The sympathetic system is not really an independent system, as was once supposed, for we now know that its ganglia have distinct relations to certain fibres which leave the spinal cord, and that its nerves, which are closely connected and freely intermix with spinal nerves, are under the control of some part of the cerebro-spinal system.

**Anatomical Elements of the Nervous Tissue. Nerve Fibres and Nerve Cells.**

The microscope shows that the nervous tissue generally consists of two structural elements, namely, nervous fibres and nervous cells. The fibres are mostly found in the nervous cords, and also in some parts of the brain and spinal cord; the cells are especially found in the cerebro-spinal centres and the ganglia of the sympathetic system although some are present at the terminations of the nerves of special senses.

A nerve is a whitish cord which is found by dissection and by microscopic examination to be made of bundles of nerve fibres running side by side, bound together and enclosed by a sheath of connective tissue. In small nerves we may find a single bundle (or funiculus) of fibres in a tubular covering, but, in larger nerves, several similar bundles (or funiculi) are united by a common covering of connective tissue. This common sheath, formed of white and elastic fibres, gives off partitions or septa which pass between the bundles of nerve fibres and support the fine blood-vessels distributed to the nerve.

Nervous fibres may be divided into two main groups, namely, medullated and non-medullated nerve fibres. Medullated fibres, examined in the fresh state, appear as glassy threads, but when treated with certain reagents each one is found to consist of a central part or axis-cylinder, which is continuous from its origin to its end, and shows a fibrillar structure under high powers. The axis-cylinder is surrounded by a sheath of white substance, or myeline, or Schwann's sheath, which is not continuous, but shows gaps known as the "nodes of Ranvier." The myeline sheath is of fatty nature and stains dark with osmic acid. It is itself surrounded by the outside envelope of the fibre or neurilemma, which is continuous, but dips down at the nodes of Ranvier. The axis-cylinder is the conducting and important part of the nerve fibre, and, as we shall see presently, it is continuous at one end with one of the processes of a nerve cell. At the central and peripheral ends of a fibre, the myeline sheath and the outside neurilemma disappear, but the axis-cylinder persists. Medullated nerve fibres or, as

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they are often termed, white nerve fibres, form the white part of the brain and spinal cord and the greater part of the nerves. They vary in size even in the same part of the nervous system, and more so in different parts, the larger being 17 microns in diameter, the smaller only 2 microns. The structure of a typical nerve fibre is shown in fig. 4. Non-medullated nerve fibres, or grey fibres, occur chiefly in branches from the sympathetic ganglia, though they are also found, to some extent, in the nerves of the cerebro-spinal system. They are transparent and soft, and are deprived of a sheath. Many of these fibres branch and unite with neighbouring fibres in their course to form a network, a peculiarity which is never present in medullated fibres.

Nerve cells are found in the grey matter of the brain and of the spinal cord, in the sympathetic ganglia, and in

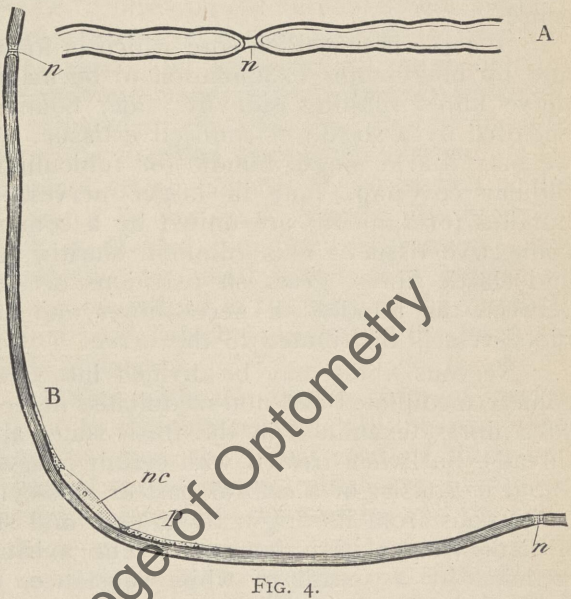


FIG. 4. TO ILLUSTRATE THE STRUCTURE OF THE NERVE FIBRES (after Huxley). (A) is a nerve fibre as it appears under the microscope with a magnification of 300 diameters and without the use of any reagent. It shows the "double contour" due to the medullar sheath and (*n*) is one of the nodes of Ranvier. (B) is a thin nerve fibre viewed under a magnification of 400 diameters after it has been treated with osmic acid. The nucleus (*nc*) with the protoplasm (*p*) surrounding the fibre beneath the neurilemma are distinctly seen together with the nodes (*n*, *n*) which limit the segment of the fibre to which the nucleus belongs.

small ganglia found on the course of some nerves. They are microscopic bodies of various shapes and sizes in different parts of the nervous system. They give off processes or poles, and may be unipolar (i.e., with one single pole or process), or bipolar or multipolar. A typical nerve cell of the multipolar variety, as found in the grey substance of the spinal cord, appears under the microscope as a nucleated mass of protoplasm having numerous branching

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processes (or dendrons or dendrites) mostly ending as fine twigs and one process, known as the axon, which does not branch and is continuous with the axis-cylinder of a nerve fibre. (See fig. 5.)

Each nerve cell, with all its processes, i.e., its dendrites and its axon (which is continued into a nerve fibre), constitutes an independent structure, and has been called a neuron. Modern researches support the view that the whole of the nervous system is a collection of neurons, each of which represents an elementary organism in itself, and is connected with others, not by anastomosis or by structural continuity, but by simple contact or contiguity.

The cells and fibres constituting the essential parts of the nervous centres are supported by a modified connective tissue termed neuroglia (or nerve-glue). It is composed of

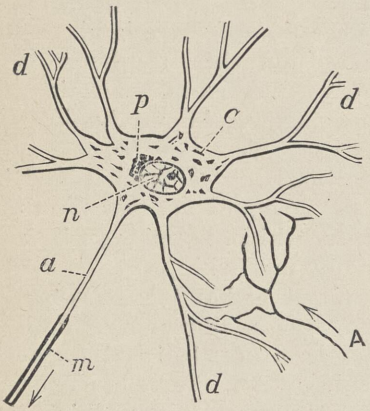


FIG. 5.

FIG. 5. DIAGRAM OF A TYPICAL NERVE CELL (FROM THE GREY MATTER OF THE SPINAL CORD). (Sherrington.) (*n*) is the nucleus, (*d*, *d*, *d*) branched dendrites; (*p*) cellular pigment; (*c*) is the cell body, mainly made of a variety of protoplasm which stains very readily; (*a*) is the axon or cylinder-axis which does not branch like the dendritic processes; it soon acquires a medullar sheath (*m*) and (outside the cord) a neurilemma. (A) represents the dendritic processes from a neighbouring cell, interlacing with but not joined on to the dendrites of the cell figured in the diagram.

cells with numerous fibre-like processes which fill up the interstices of the true nervous elements, namely, fibres and cells. Further support is given (1) by ramifications of the ciliated epithelium lining the central canal of the spinal cord and the cavities (or ventricles) of the brain which communicate with the central canal of the spinal cord; (2) by the connective tissue of the brain and spinal cord (or pia mater) which sends in delicate partitions carrying the blood-vessels which are necessary to insure the life of the nervous tissue.

While the chief function of a nerve fibre is to conduct nervous impulses, nerve cells may not only conduct and transfer impulses, but they may modify or even originate nervous impulses of various kinds.

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**Classification of Nerve Fibres. Various Kinds of Nerves.**

According to their function, nerves and nerve fibres are classified into: (a) afferent or centripetal, and (b) efferent or centrifugal. Nerve fibres which convey impulses from a nervous centre to some part of the body are efferent or centrifugal fibres, while fibres which convey impulses to a nervous centre from some part of the body are afferent or centripetal. The term motor is sometimes used instead of efferent because many of the impulses conveyed from the nervous centres to the peripheral organs of the body determine the contraction of a muscle, i.e., production of movement. Likewise, the term sensory is often used instead of afferent because an impulse sent to the nervous centres from a peripheral organ gives rise to a sensation. However, the terms afferent and efferent are much more satisfactory, since efferent fibres do not necessarily end in a muscle; they may, for instance, end in a gland, in which case an impulse conveyed from the nervous centre will evoke the secretion of that gland. Again, impulses passing along fibres from the periphery to the nerve centres do not necessarily give rise to sensation, but may, as we shall see presently, cause the production of a reflex action.

The various nerves of the body are often classified into somatic and splanchnic nerves. Somatic nerves (from the Greek *soma,* body) are nerves which supply such body-structures as the muscles, bones, skin, etc., whereas splanchnic nerves (from the Greek splanchna, viscera) are distributed to the viscera, heart, lungs, alimentary canal, etc. Broadly speaking, somatic nerves proceed directly from the nervous centres to the structures they serve to innervate, while the viscera are supplied by nerve fibres which leave the spinal cord in the form of medullated fibres, run forwards into the ganglia of the sympathetic system, where they lose their sheaths and whence they issue as non-medullated fibres.

**The Nervous System Generally.**

The afferent (or sensory) and the efferent (or motor) nerves, and the central organs (cerebrum, spinal cord and sympathetic ganglia), constitute the greater part of the nervous system which, with its function of innervation, we must now study a little more closely and as a whole.

The cerebrum and the spinal cord lie in the cavity of the skull and central canal of the vertebral column, the bony walls of which are lined by a tough fibrous membrane serving as the periosteum of the component bones, and called the dura mater. This membrane is made of a thick layer of densely woven fibres of connective tissue with which a small

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amount of elastic tissue is mixed. The cerebrum and the spinal cord themselves are closely invested by a very vascular membrane of fibrous connective tissue called the pia mater, which carries the numerous blood-vessels supplying the nervous substance. Between the dura mater and the pia mater lies another delicate membrane called the arachnoid. The three membranes are connected with each other at various points, and the arachnoid, which is not only delicate but also less regular than the other two, divides the space between the dura mater and the pia mater into two spaces containing a fluid and lined by a delicate epithelium. The space between the dura mater and the arachnoid is termed the subdural space; the space between the arachnoid and the pia mater is the sub-arachnoid space. The fluid contained in the above spaces is termed cerebro-spinal fluid; it resembles ordinary lymph, but it does not clot as true lymph does.

**Spinal Cord and Spinal Nerves.**

The spinal cord is the mass of nervous matter contained in the spinal canal which is formed by the superimposed rings of the vertebræ. It is 42 to 45 cms. long, a little less than 2 cms. in diameter, and reaches from the margin of the circular opening in the occipital bone (foramen magnum) to the first lumbar vertebra, where it ends in a slender thread, the filum terminale or terminal thread, which lies among a mass of nerve roots termed the horse-tail or *cauda equina*. At its upper end, the spinal cord is continued into the bulb, or *medulla oblongata,* which lies within the cavity of the cranium.

Passing out of the cord at intervals on each side are the thirty-one pairs of spinal nerves, the first pair coming off between the skull and the first vertebra or atlas, the next pair between the atlas and the second vertebra or axis, and so on.

The spinal nerves leave the bony canal by apertures between the vertebræ (inter-vertebral foramina) and are distributed to the muscles and the skin generally. The lower pairs come off close together from the lower end of the cord, and pass downwards in the *cauda equina* to be distributed to the lower limbs.

The diameter of the cord is not uniform throughout, being marked by two enlargements, the upper one being in the cervical region, the lower one in the lumbar region. Two fissures run along the length of the cord and separate it into a right and a left half. The anterior median fissure is wider but not so deep as the posterior median fissure. (See fig. 6.)

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Each spinal nerve originates from the cord by two roots, and consequently there are twice as many roots as there are spinal nerves. After their exit from the spinal canal the two roots join together to form the main trunk of the nerve, but before doing so, the posterior root presents an enlargement called the ganglion of the posterior root.

A transversal section of the spinal cord shows that it is made of two substances, a white matter on the outside, which gives the cord its white, opaque appearance, and a greyish red matter in the interior. This grey matter, as it is called, is so arranged that in a transversal section it looks, in each

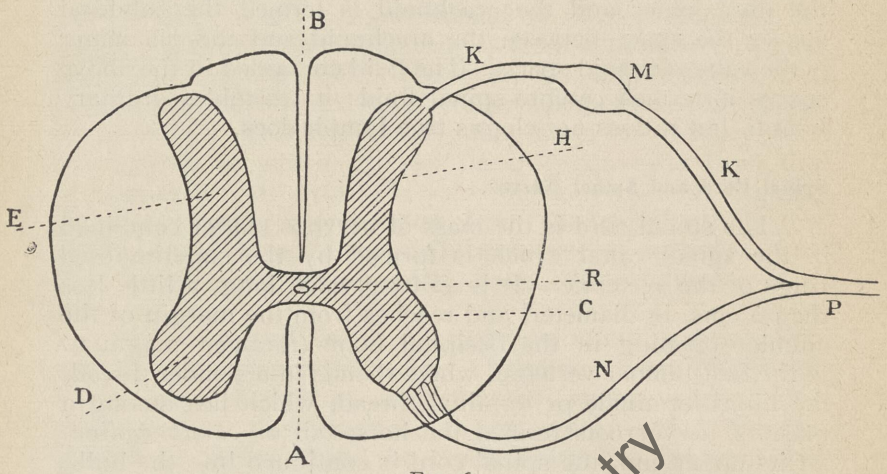


FIG. 6.

FIG. 6. DIAGRAMMATIC SECTION OF THE SPINAL CORD AND ROOTS OF THE SPINAL NERVES. The shaded portion of the diagram represents the grey matter which occupies the central part and is surrounded by white matter. The cord is divided into two symmetrical halves by a medial antero-posterior fissure made of two parts, namely (1) the posterior fissure (B) which is narrow and extends deeply up to the bridge of grey matter (or grey commissure) which connects the grey matter of the two lateral halves of the cord. (In the diagram, the posterior fissure (B) does not extend, as it should, as far as the grey commissure.) The central canal of the spinal cord is shown at (R), occupying the middle of the grey commissure : (2) the anterior fissure (A) which is wider and less deep than the posterior one. It does not extend, like the latter, as far as the grey commissure but ends at a bridge of white matter (the white commissure) which connects the right and the left portion of the white matter of the cord.

Note the crescentic appearance of the grey matter in each lateral half of the cord ; (E) and (D) represent the posterior and anterior horns of the grey matter in the left half, while (H) and (C) are the similar parts in the other half. The two crescents are united by the grey matter we have alluded to under the heading of grey commissure.

From the grey matter of the anterior horn on each side, nervous fibres pass out and constitute the anterior root (N) of a spinal nerve. From the grey matter of the posterior horn nervous fibres proceed to form the posterior root (K) of the nerve. The two roots join together to form the trunk (P) of a spinal nerve. Note the swelling or ganglion (M) on the path of the posterior root.

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half, somewhat like a crescent with one end bigger than the other, and with the concave side turned inwards. (See fig. 6.) The two ends of each crescent are called its horns or cornua, the one directed forwards being the anterior horn or anterior cornu, the one directed backwards, the posterior horn or posterior cornu. The convex sides of the crescents of the grey matter approach one another and are joined by a bridge of the same matter, which contains the central canal of the cord, and is called the grey commissure. The grey commissure is separated from the inner end of the anterior fissure by a thin bridge of white matter which forms what is called the white commissure.

As already pointed out, there is a fundamental difference in the structure of the grey and white matter. The white matter consists almost entirely of nerve fibres, supported in a delicate framework of neuroglia, and accompanied by blood-vessels. Most of these fibres run lengthways in the cord, and consequently in a transversal section, the white matter is really composed of a multitude of the cut ends of these fibres. The grey matter, on the other hand, contains, in addition, a number of nerve cells, some of which are of considerable size (as much as 100 microns, i.e., 1-10th of a millimeter, in the anterior horn of the cord). Nervous cells are wholly, or almost wholly, absent in the white matter. Many of the nerve fibres contained in the anterior root of a special nerve can be traced to the nerve cells of the anterior horn, while those of the posterior root, for the most part, pass towards the posterior horn.

We have alluded just now to the ganglion or swelling found on the posterior root of each spinal nerve. Microscopic examination shows that this ganglion consists of an external sheath of connective tissue which encloses a group of large nerve cells, generally pear-shaped and unipolar. The nerve fibres which enter the distal end of the ganglion divide, one branch becoming attached to the process of one of the cells of the ganglion, the other one continuing its way to pass on into the grey matter of the posterior horn. Thus the fibres of the posterior root of a spinal nerve, instead of passing directly into the grey matter of the cord as is the case for those of the anterior root, present a T-shaped arrangement, the nerve cells of the ganglion appearing to be lateral appendages of the nerve fibres.

**The Function of the Two Roots of a Spinal Nerve.**

If the trunk of a spinal nerve be irritated in any way, as by pinching, cutting, galvanising, or applying a hot body or a proper chemical reagent, two things happen: (1)

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all the muscles to which filaments of the nerve are distributed contract, and (2) pain is felt, the pain being referred to that part of the skin to which the fibres of the nerve are distributed. In other words, the effect of irritating the trunk of a nerve is the same as that of irritating its component fibres at their terminations. The effects just described will follow upon irritation of any part of the branches of the nerve, except that when a single branch is irritated the only muscles affected, and the only region of the skin to which pain is referred, will be those to which that particular branch sends nerve fibres. And these effects will follow upon irritation of any part of a nerve, from its smallest branches up to the point of its trunk where the anterior and posterior roots unite with each other.

If the anterior root only is irritated in the same way, only half the previous effects are brought about, i.e., all the muscles to which the nerve is distributed contract, but no pain is felt.

Again, if the posterior root be irritated, only half the effect of irritating the whole trunk is produced, only it is the other half; that is to say, none of the muscles to which the nerve is distributed contracts, but pain is felt and is referred to the whole area of skin to which the fibres of the nerve are distributed.

These facts show clearly that all the power of causing muscular contraction which a spinal nerve possesses is lodged in the fibres which compose the anterior root, and all the power of giving rise to sensation in those of the posterior root. The same conclusion may be arrived at in a different way. If, in a living animal, the anterior root of a spinal nerve be cut, the animal loses control over the muscles to which the nerve is distributed, though the sensibility of the region of the skin supplied by the nerve is perfect. If the posterior root is cut sensation is lost, though the power of voluntary movement remains. If both roots be cut, neither sensibility nor voluntary movement is any longer possessed by the part supplied by the nerve. The muscles are said to be paralysed, and the skin may be cut or burnt without any sensation being excited.

If, when both roots are severed, that end of the anterior root which remains connected with the trunk of the nerve be irritated, the muscles contract, while if the other end be so treated, no apparent effect results. On the other hand, if the end of the posterior root connected with the trunk of the nerve be irritated, no apparent effect is produced, while if the end connected with the cord be irritated, pain immediately follows. When no apparent effect follows upon

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irritation of any nerve, it is not probable that the molecules of the nerve remain unchanged. On the contrary, it seems that the same change occurs in all cases, but an efferent or motor nerve is connected with nothing that can make that change apparent save a muscle or a secreting gland, and an afferent or sensory nerve with nothing that can show an effect but the central nervous system.

**Degeneration of a Spinal Nerve.**

We have pointed out that a fibre of the anterior root of a spinal nerve is really the prolongation of the axon of a nerve cell in the anterior horn of the grey matter of the spinal cord, and it is not astonishing to find that the continued life of any efferent (or motor) fibre is dependent upon the continuance of its connection with the cell from which it arises. The proof of this dependence is afforded by cutting an efferent nerve and preventing the cut ends from reuniting. It is found that shortly after the operation, those parts of the nerve whose connection with the spinal cord has been severed (i.e., the peripheral portion of the nerve) undergo what is termed degeneration. This degeneration shows itself by structural changes in the nerve fibres. The medulla or Schwann's sheath breaks up into oily drops which are absorbed into the surrounding tissues and ultimately disappear. The axis-cylinder also breaks up into pieces, which are likewise absorbed, and all that is left is a sort of skeleton fibre made of the primitive sheath or neurilemma with the septa or partitions originating from it. While these structural changes take place, and even before they become obvious, the irritability of the nerve becomes gradually less, so that soon the nerve makes no response to any stimulus which may be applied to it. Complete degeneration of a severed nerve takes about ten or twelve days. Degeneration of a nerve after section is often called, from its discoverer, Wallerian degeneration.

It must be clearly understood that in the case of an efferent (or motor) nerve, degeneration does not occur in the part of the nerve which is still connected with the spinal cord (central part), the changes which characterise the process of degeneration being restricted to the peripheral portion of the nerve, i.e., to the portion which is no longer connected with the spinal cord.

If the same method of experiment is applied to the posterior root of a spinal nerve, the results are somewhat different. If the root is cut at a point between the ganglion and the junction of the anterior and posterior root, the afferent fibres degenerate from the point of section to the

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end of the various branches of the nerve, but if the section is made between the spinal cord and the ganglion, then the part of the root which lies between the section and the cord degenerates, whereas the portion still connected with the ganglion does not. This shows that whilst the life of the nervous fibres of the anterior root (efferent or motor fibres) depends upon their connection with the cells of the grey matter of the spinal cord, the life of the fibres of the posterior root (afferent or sensory fibres) depends upon their connection with the ganglion of that root. In other words, the function of the ganglion of the posterior root is to provide for the nutrition of these afferent nerve fibres, which may be regarded as originating from the nerve cells of the ganglion.

The result of the above experiment is shown diagrammatically in fig 7, in each part of which K represents the posterior root of a spinal nerve with the ganglion M; N is the anterior root, and P the trunk of the nerve. The section is shown at S, and the degeneration is indicated by shaded lines. In the first part of the diagram the section involves the whole of the trunk of the nerve and all the afferent and efferent fibres of the portion of the nerve separated from the cord degenerate, the degeneration extending gradually from the point of section towards the periphery of the body. In the second part of the diagram, in which the anterior root is cut at S, there is a similar degeneration which is, however, restricted to the portion of the root which is no longer connected with the cord, and which gradually extends to the motor fibres only of the trunk of the nerve. In the third part of the diagram the section is made on the posterior root in the portion between the ganglion M and the trunk of the nerve. The result is similar to that of the previous case, except that the degeneration involves the part of the posterior root which is no longer connected with the ganglion and to the afferent fibres of the trunk of the nerve. In the fourth part of the diagram, the section of the posterior root is made between the cord and the ganglion; the degeneration is localised to the portion of the root separated from the ganglion, and extends from S towards the cord.

This experimental method for the determination and the localisation of the nutritional centres from which nerve fibres originate is known as the "degeneration method" or the "Wallerian method." It has proved most useful in determining the various tracts or paths in the spinal cord and the brain, along which nervous impulses of various kinds pass, as we shall see later on.

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It will be observed that in the experiment referred to just now, there is evidence that when a nerve is irritated, there is a something that is propagated along the nerve fibres; this something, which is spoken of as a nervous impulse, probably consists of a change in the arrangement

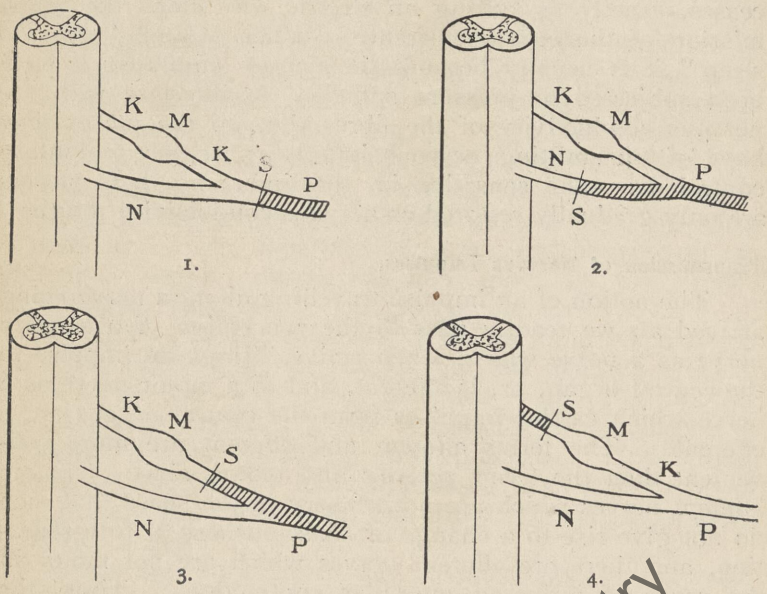


FIG. 7.

FIG. 7. ILLUSTRATING THE WALLERIAN DEGENERATION OF THE ROOTS OF SPINAL NERVES. In all the four parts of the figure, (K) represents the posterior root of a spinal nerve with its ganglion (M), (N) is the motor root and (P) the trunk of the nerve. The first part of the diagram shows the degeneration of the afferent and efferent fibres of the entire nerve following a section of the trunk of the nerve at the point (S). The degeneration, which is shown by the shaded part of the figure, extends gradually all along the nerve from the point of section away from the cord. The second diagram shows the degeneration of the efferent or motor fibres only, due to a section of the anterior root at (S). The drawing is slightly inaccurate, inasmuch as only the half of the trunk (P) which is made of the motor fibres derived from the anterior root should be shaded to indicate that the degeneration occurring in this case is limited to the motor fibres of the trunk of the nerve. The third diagram indicates schematically the effect of cutting the posterior root at (S), i.e., farther away from the cord than the ganglion (M). Here again the degeneration progresses from the point of section along the path of the nerve trunk but this degeneration only occurs in the portion of the nerve made of the afferent or sensory fibres, a fact which is not clearly indicated in the diagram.

The fourth part of the figure shows the effect due to a section of the posterior root at any point (S) between the cord and the ganglion (M). Only the portion of the posterior root remaining attached to the cord gradually degenerates, the trunk of the nerve and the portion of the posterior root between the ganglion and the trunk itself, as well as the anterior root, not being affected.



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of the molecules of the fibres. If a motor or a sensory nerve be irritated at any point, contraction of the muscles of the part supplied, or sensation or some corresponding event in the central organ, immediately follows. But if the nerve is cut or even tightly tied at any point between the part irritated and the muscle or the central organ, the effect ceases, exactly as cutting an electric wire stops the transmission of the electric current. When a limb "goes to sleep" it is usually because the nerves supplying it have been subjected to pressure sufficient to interfere with the nervous conductivity of the fibres, i.e., to the power they have of transmitting nervous impulses; we lose voluntary control over, and sensation in, the limb, and these powers are only gradually restored as nervous conductivity returns.

**Transmission of Nervous Impulses.**

The notion of an impulse travelling along a nerve being arrived at, we readily pass to the conception of a sensory nerve as a nerve which, when active, brings an impulse to the central organ, or, is afferent, and of a motor nerve as a nerve which carries impulses from the central organ, or, is efferent. The terms afferent and efferent are more convenient than the terms sensory and motor, since there are afferent nerves which are not sensory in the sense that they do not give rise to a change of consciousness or to a sensation, and there are efferent nerves which are not motor in the sense of inducing muscular contraction. Thus, the nerves by which electrical fishes give rise to an electrical discharge from some special organs to which these nerves are distributed are efferent, inasmuch as they carry impulses from the nervous centres to the electric organs, but they are not motor, inasmuch as they do not cause muscular contraction. The pneumogastric nerve (the 10th pair of cranial nerves) to which we shall refer presently, when it stops the beating of the heart cannot be called motor, and yet it is then acting as an efferent nerve. Likewise, the nerves which supply the cells of a gland and cause them to secrete are not motor in the strict meaning of the term, but they are efferent as regards the direction in which they convey their impulses.

It must be understood that the use of the terms afferent and efferent does not imply that if a nerve is irritated in the middle of its length the impulse set up in it travels only towards the nervous centres if the nerve is afferent, or away from it if efferent. On the contrary, there is evidence that in either case the impulse travels both ways, and all that is meant is that the afferent nerve from the arrangement of

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its two ends, in the skin or other peripheral organ on one hand, and in the nervous centres on the other hand, is of use only when impulses are travelling along it from the periphery towards the nervous centres, and similarly an efferent nerve is of use only when impulses are travelling along it away from the nervous centres towards the peripheral organs.

Though afferent nerves apparently convey impulses in one direction only, namely, from the periphery of the body to the nervous centres, and efferent nerves from the nervous centres to some peripheral organs, e.g., muscles, it is possible to show experimentally that nerves of either kind are capable of transmitting impulses in both directions, although in one of these directions in each case, no effect is manifest. The experimental proof in the case of an afferent or sensory nerve, has been given by the French physiologist, Paul Bert. He grafted the tip of a rat's tail to the back or to the nose of the animal, and when union had been effected, he amputated the tail near its original base. The rat was then provided with a trunk-like appendage on its back or its nose, and gave evidence of sensation if this appendage was pinched. Under these circumstances, sensory impulses passed from base to tip of the tail, whereas formerly in the ordinary way, they passed from tip to base.

It has been ascertained that electrical phenomena occur in nerves (whether afferent or efferent) when an impulse is conveyed through them and this electrical disturbance or this current of action, as it is generally termed, may be used to give a proof of the fact that nerves of either kind transmit impulses in both directions, and that if no effect is manifest in the peripheral portion of a sensory nerve or in the central portion of a motor nerve, it is merely because a sensory impulse can only be perceived by a nervous centre and a motor or efferent impulse can only be manifested by a muscular contraction or by some similar effect.

There is no difference in structure or physical character between afferent and efferent nerves. We know but little of the nature of a nervous impulse. We know that it may be started in a nerve by various artificial means such as pinching, or knocking the nerve, or by suddenly warming or cooling it, and most readily by stimulating the nerve electrically, and we suppose that, by any of these means, there is set up in the nerve to which any of the above stimuli is applied, a disturbance which is then propagated in succession from one particle of the axis-cylinder to the next, so that it ultimately reaches a point in the nerve remote from

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that in which it was started. In this way, we speak of a nervous impulse as due to the propagation of a molecular disturbance, though the expression does not convey anything as to the true nature of the phenomenon.

**Speed of Propagation of Nervous Impulses.**

The impulse which travels along a nerve requires a certain time for its propagation, and is vastly slower than many other movements, even slower than sound. The rate of transmission can be determined by means of a muscle-nerve preparation similar to that which we have described in the paragraph devoted to Muscular Contraction. The gastrocnemius muscle of a frog is carefully dissected, and as long a portion as possible of the nerve supplying it (the sciatic nerve) is left attached to it. The preparation is arranged as shown in fig. 8, the muscle being fixed at one end and being kept in slight condition of stretch by a weight

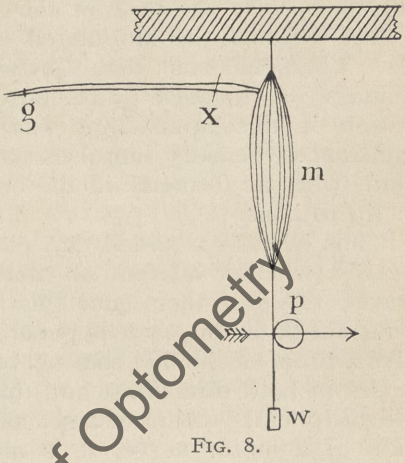


FIG. 8.

FIG. 8. DIAGRAMMATIC ARRANGEMENT OF A MUSCLE-NERVE PREPARATION TO DETERMINE THE VELOCITY OF PROPAGATION OF NERVOUS IMPULSES. The muscle (m) (say the gastrocnemius nerve of a frog) is dissected, a fairly long portion (g x) of the nerve supplying it (the sciatic nerve) being left connected with the muscle itself. The rest of the apparatus is similar to that we have described in FIG. 2. An electric shock of instantaneous duration is applied first at the point (g) of the nerve and the exact moment the muscle begins to react is registered by the lever on the revolving drum. Then a similar shock is applied at (x) and again the moment the muscle reacts is registered. It is found that the time interval before the muscular reaction begins when the shock is applied at (g) is longer than the similar interval following a shock applied at (x). The difference between these two intervals of time, which is easily ascertained from the time curve registered by a vibrating tuning fork, represents obviously the time the nervous impulse takes to travel from (g) to (x), i.e., through a known length of nerve.

(w) attached to the tendon at the other end. The sciatic nerve (xg) is so disposed that it may be stimulated either at a point (x) as close as possible to its entrance in the muscle, or at a point (g) as far away as possible from the muscle. It is found that if the nerve is stimulated at (x) the muscle contracts practically at once, this contraction being shown by a rapid movement of the free end of the pointer. Then, the nerve is stimulated at the point (g) as far as possible from

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the muscle, and it is found that the contraction of the muscle occurs after a certain interval of time which can be accurately measured by means of a device (tuning-fork) similar to that used in the study of the muscular contraction. Let us suppose that in an experiment of this kind, the contraction of the muscle in answer to a stimulation of the nerve at the point (g) has taken, say, 1-500th of a second longer than when the stimulation was applied at (x). This difference can only be due to the fact that when the impulse is started at (g) it takes 1-500th of a second longer to reach the muscle than when started at (x). Since the length of the piece of nerve between (x) and (g) can be known by direct measurement (let it be, say, 6 cms.), the speed of propagation can be easily calculated. In this way it is found that a nerve impulse travels at the rate of about 28 to 30 metres per second in the nerve of a frog.

The rate of propagation of a nervous impulse depends on the temperature of the nerve, and diminishes as the nerve is cooled; in the case of a frog's nerve, the rate may be reduced by cooling to as little as 1 metre per second. Hence, it is not surprising to find, in experiments made on the nerves of warm-blooded animals, a higher rate of transmission (something like 33 metres per second) than in the case of a cold-blooded frog.

**Physiological Properties of the Spinal Cord.**

Up to the present we have only experimented on nerves. We may now test in a similar way the properties of the spinal cord. If the cord is cut across, say, in the middle of the back, the legs, and all the parts supplied by nerves which come from the cord below the section, will be insensible, and no effort of the will can make them move. The parts supplied by nerves emerging from the cord above the section retain their ordinary powers.

If, when the cord is cut across, the cut end of the portion below the section is stimulated, violent movements of all the muscles supplied by nerves given off from the lower part of the cord take place, but no sensation whatever is felt by the brain. On the other hand, if the cut end which is still connected with the brain, or if any afferent nerve connected with the part of the cord above the section be irritated, sensation ensues as shown by the movements of the animal on which the experiment is performed, but in these movements the muscles supplied by nerves coming from the cord below the cut take no part. This shows that the cord may be regarded as a great mixed motor and sensory nerve. From the structural connections of the spinal cord with

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various parts of the body through the thirty-one pairs of spinal nerves, referred to previously, it is clear that sensory or other afferent nerve impulses from the periphery in the trunk and limbs can only be conveyed to the brain and there perceived when the cord is uninjured and intact. The mandates of the will, originating in the brain, can only pass to their destination along the efferent nerves when the communication through the cord is uninterrupted by injury or disease. Any disease or injury that affects the whole of the cord leads to paraplegia, or complete paralysis, with loss of sensation and voluntary movement in the parts of the body which receive their nerve supply from the portion of the cord below the injury.

Besides being a huge mixed nerve, motor and sensory, the spinal cord is an important centre of reflex action. We have seen that if the trunk of a spinal nerve be cut so as to sever its connection with the cord, the part of the body in which the nerve is distributed loses all power of movement and all sensibility; this part of the body becomes entirely paralysed. If, however, the cord is completely cut across so as to sever its connection with the brain, irritation applied to the skin of the parts supplied with afferent (or sensory) nerves from the portion of the cord below the section, though it does not give rise to sensation, produces violent motions of the parts supplied with efferent (motor) nerves from the same portion of the cord. Thus, in the case of a man whose legs are paralysed and insensible from spinal injury, tickling the soles of the feet will cause the legs to kick out convulsively. In a broad way, so long as both roots of the spinal nerves remain connected with the cord irritation of any afferent nerve is competent to give rise to excitement of some or the whole of the efferent nerves so connected. If the cord be cut across a second time at any distance below the first section, the efferent nerves below the second cut will no longer be affected by irritation of the afferent nerves above, but only of those below, the second section; or, in other words, in order that an afferent impulse may be converted into an efferent one by the spinal cord, the afferent nerves must be in uninterrupted material communication with the efferent nerves by means of the substance of the spinal cord.

**Reflex Actions of the Spinal Cord.**

This peculiar power of the cord, by which it is competent to convert afferent into efferent impulses is that which distinguishes it physiologically as a central organ, a nervous centre, from a mere nerve.

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Speaking generally, the whole of the activities of the nervous centres are divided into reflex acts and voluntary acts. A reflex action is the immediate efferent response to afferent impulses, independently of the will. The spinal cord possesses this power of responding to afferent impulses in a remarkable degree and may, in fact, be regarded as formed in part of a number of reflex centres. It also acts as a conductor of impulses via the spinal nerves to and from the brain. As we shall see presently, the brain itself may also become a centre of reflex action, but there is no doubt that most of the reflex acts which play such an important part in daily life are performed through the spinal cord.

The power of the cord to originate reflex action is localised in the grey matter and not in the white substance. The mechanism of a reflex action involves the following elements: (a) a sensient surface or a peripheral sense organ; (b) an afferent nerve fibre; (c) a cell or group of cells on the afferent tract; (d) a connection of these cells (commissural fibres) with (e) efferent fibres; (f) a muscle or a gland or other organ capable of response to the stimulus from the nerve centre involved in (c) and (d). These are the components of a reflex arc.

An appropriate stimulus applied to the sensient surface passes along the afferent fibres and leads to a discharge of efferent impulses which set the muscle or other responding organ in action. Thus, a frog whose brain has been removed or severed from the cord will remain at rest, but if the skin be irritated by a prick or other stimulus, its limbs will be set in motion by the contraction of certain muscles.

The reflex process thus set up is shown diagrammatically in fig. 9. From the sensient surface (a) an afferent impulse

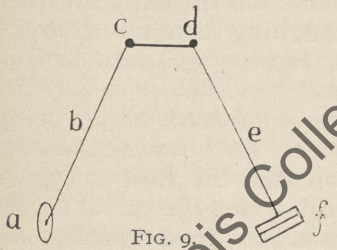


FIG. 9. MECHANISM OF A REFLEX ACTION (after Waller). (a) represents diagrammatically a sensorial organ, say a cell in the skin, to which a stimulus is applied; (b) is an afferent or sensory fibre travelling from (a) to the posterior portion of the grey matter of the cord and ending in a nerve cell (c) in the posterior horn. In some unexplained way, the impulse passes across the grey matter of the cord to one of the large cells of origin of the anterior root (in the anterior horn) represented by (d). The cells of the anterior root are connected by efferent fibres (e) with a muscle (f) which then reacts to the irritation or to the stimulus applied to the sensory organ (a).

passes along (b) to the posterior root of the spinal cord, the nerve fibres of the posterior root ending in minute filaments

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among the cells of the posterior horn at (c). In some unexplained way, the impulses pass across the grey part of the cord to the large cells of the anterior horn (d). The cells of the anterior horn are connected through their axons with the efferent fibres (e), and these convey the stimulus to the muscle or the responding organ (f). It should be noted that the centre in the cord does not merely reflect the afferent impulses into efferent impulses; the reflex act often seems to be adapted for a purpose, and to be of a useful nature. If a person is asleep or even very deep in thought, and a slight irritation is applied, as, for instance, by gently touching the skin of the face with a feather, he will without waking or without thinking about it, put up his hand to brush the irritation away. Again, in the case of the brainless frog referred to just now, if a drop of an irritating fluid is put on the skin, the movements of the animal are directed to removing the offending substance. As is well known, winking movements and excessive secretion of the lachrymal gland, both of a reflex nature, occur on irritation of the conjunctiva by a foreign body in the conjunctival sac, as we shall see more fully presently. Likewise, a reflex closure of the lids follows on the sudden approach of a missile. Sneezing and coughing are other instances of reflex movements of a similar nature which are performed for a definite purpose and without the intervention of the will. In a typical reflex action, afferent impulses reach a nerve centre and are converted by the irritable protoplasm of the centre into efferent impulses. There is often a close relation between the strength of the original stimulus applied to the afferent nerve and the magnitude of the efferent impulse, but a very slight stimulus may also be intensified in a nerve centre, where the arrangement of the reflex mechanism is so complex that the result is the contraction of many muscles. Witness the convulsive fit of coughing determined by a minute particle passing into the larynx, or the start we experience on production of a sudden noise.

As we have already stated, the spinal cord, beside being a centre for reflex action, serves to the transmission of nervous impulses between the brain and the various organs such as the muscles and the skin with which the spinal nerves are connected. In fact, the cord acts as a great mixed motor and sensory nerve. When we move a foot certain nervous impulses starting in some part of the cerebral hemisphere pass along the whole length of the cord as far as the roots of the spinal nerves going to the legs and, issuing along the fibres of the anterior bundle of these roots, find their way to the muscles which move the foot. Likewise, when the sole of

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the foot is touched afferent impulses travel in the reverse way upwards along the spinal cord to the brain.

The question which naturally arises is: In what manner do those afferent and efferent impulses travel along the spinal cord? The question is a difficult one, and indeed, a complete statement on the subject is not possible in the actual state of science. Our present knowledge of the paths of impulses in the cord has mainly been obtained by means of the degeneration method. We have seen that when a nerve is cut, its fibres degenerate. Since this degeneration, which manifests itself by the structural changes we have mentioned, indicates a breakdown in the proper nutrition of the fibres in which it occurs, it may be used to determine the relationship of the nerve fibres to the centres upon which their nutrition depends.

The whole white matter of the cord is composed of fibres similar to those of an ordinary medullated nerve, and these fibres degenerate when cut off from the centres on which their nutrition depends. Hence, if the spinal cord is completely cut across, or, if transverse cuts are made into any part or the whole of any one or more of the columns of white matter of which the cord is so largely made up, degenerative changes start from the point of section and, by the course they pursue up and down the cord, enable us to follow the path of certain fibres in that white matter. The degenerative changes which take place in parts of the white matter both above and below the point of section only affect limited parts of the white matter, and the parts thus affected above the cut, i.e., towards the brain, are different in position from the parts affected below the cut. The changes which start above the cut and extend upwards towards the brain, are spoken of as "ascending degenerations," those of which are observed to occur downwards are termed "descending degenerations." Moreover, since the parts which degenerate are limited as to their transverse sectional area while running for very considerable distances along the white matter of the cord, they are usually spoken of as "tracts," and since these tracts serve definitely for the transmission of impulses up and down the cord, they denote very definite paths of conduction along the spinal cord.

We shall have occasion later on to see how the degeneration method has been used to determine the path of visual impulses from the retina to the brain.

**General Arrangement of the Brain.**

The brain, or cerebrum, is a very complex organ which occupies the cavity of the skull or cranium, and is thus

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placed at the upper end of the spinal cord, with which it is connected by means of the spinal bulb or simply the bulb (medulla oblongata). This latter structure passes gradually into, and in its lower part, has very much the same structure as, the spinal cord itself.

A complete description of the brain is beyond the scope of this work. We shall give below some of the details which can be ascertained from examination of good drawings as found in most text-books on anatomy, or better still, from a careful study of a papier mâché model of the human brain of average size. These details are given below more for the purpose of reference than for actual study.

Before proceeding to this investigation, it is well to have a general idea of the main arrangement of the brain, and of the various parts which play an important part in the working of the eye. The division of the cerebro-spinal centres (brain proper and spinal cord), is based upon the embryological development of these organs.

**Embryological Development of the Brain.**

The cerebro-spinal nervous centre makes its first appearance as two ridges of ectoderm bordering a groove in the median line of the upper aspect of the embryo (fig. 10, A). As these ridges increase in elevation they soon meet over the back of the groove, which ultimately becomes a canal termed the neural canal (fig. 10, B, C, D). At this period the

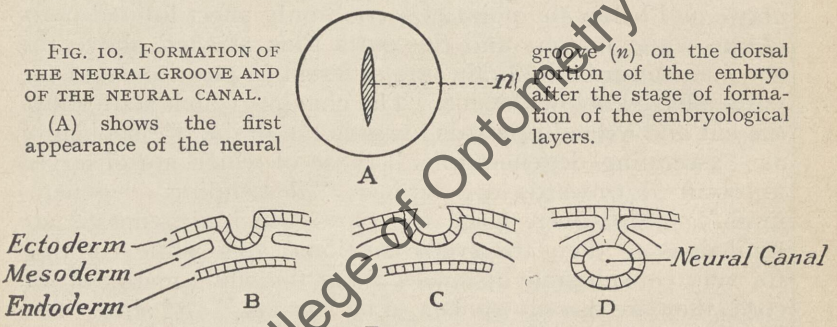


FIG. 10. FORMATION OF THE NEURAL GROOVE AND OF THE NEURAL CANAL.

(A) shows the first appearance of the neural groove (*n*) on the dorsal portion of the embryo after the stage of formation of the embryological layers.

(B) represents to a larger scale and in diagrammatic form a transversal section of the embryo showing how the ectoderm becomes folded in, to constitute the neural groove.

(C) shows a further stage in the development of the neural groove, and (D) represents the neural canal which ultimately becomes separated from the superficial ectoderm and thus constitutes an internal tube, of ectodermic origin, which runs along the embryo.

embryonic nervous system may be represented as a cylinder whose walls are made of ectodermic cells; in this stage it is called the neural axis. While the great majority of the cells

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become differentiated into neurons with their supporting tissue, the neuroglia or nerve-glue, some of them remain as a lining to the canal and form what is called the ependymal epithelium. The neural canal persists throughout life under different names, and assumes different forms in different portions of the cerebro-spinal centres; we have already alluded to the central canal of the spinal cord, which is continuous upwards with spaces in the brain itself which are called the ventricles of the brain.

That part of the neural axis which is contained within the embryonic skull, and which is to become the brain proper, is seen at a very early stage to be dilated into three sacs or vesicles, known, from behind forwards, as the hinder brain (rhombencephalon), the middle brain (mesencephalon) and the fore-brain (prosencephalon) (fig. 11). A little later the first and third of these vesicles are differentiated into two

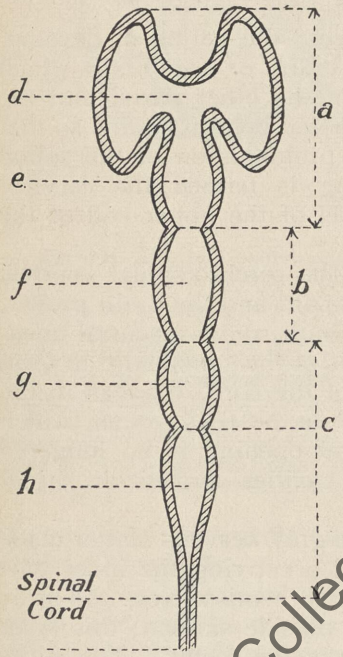


FIG. 11.

FIG. 11. TO ILLUSTRATE DIAGRAMMATICALLY THE DEVELOPMENT OF THE BRAIN. At an early period of development, when the posterior part of the neural canal is still open, the anterior portions of its walls dilate considerably but at first remain single. The walls of the tube soon show two constrictions which divide the embryo brain into the anterior, the middle and the posterior primary cerebral vesicles represented by (*a*) (*b*) and (*c*) respectively. The anterior vesicle is often termed Prosencephalon or fore-brain; the middle one is called the Mesencephalon or mid-brain and the posterior one, the hind-brain or Rhombencephalon, owing to its rhomboidal shape.

The anterior vesicle soon divides into the Telencephalon or end brain (*d*) which will ultimately become the cerebral hemisphere, and the Diencephalon or inter-brain (*e*) which will form the optic thalami, the corpora geniculata, the pineal body and the optic tracts.

The middle vesicle will develop into the mid-brain containing amongst other structures the corpora quadrigemina. The posterior primary vesicle will form the metencephalon or after brain which ultimately develops into the cerebellum (*g*) and the myelencephalon which will become the bulb (*h*) and is continued posteriorly into the spinal cord.

each, the hind part forming the myelencephalon or marrow brain (which will ultimately become the bulb or connecting link between the spinal cord and the portion of the brain located in the skull) and the metencephalon or after brain which will form the cerebellum or small brain.

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The middle vesicle or mid-brain or mesencephalon remains single and will ultimately become the corpora quadrigemina.

The fore-brain (prosencephalon) or anterior primary cerebral vesicle develops into the end brain, which will form the cerebral hemispheres and the inter-brain or diencephalon, which will give rise to the optic thalami, the geniculate bodies, the pineal body and the optic tracts.

Fig. 10 (B, C, D) shows diagrammatically the formation of the neural canal by invagination, i.e., folding in of the ectoderm on the middle of the upper part of the embryo, and fig. 11 shows, also in diagrammatic form, the various cerebral vesicles derived by the development, multiplication and differentiation of the cells forming the walls of the neural canal.

Fig. 12 is a sagittal section of the brain of a mammal at a later stage of development.

In the human body, and during the period of development, the anterior part of the brain or fore-brain which increases in size much more than the other parts, and the portion in front of the myelencephalon bend forwards so that they are no longer in the direct prolongation of the spinal cord. This knee-shaped bending is termed the cervical flexure, since it occurs at the level of the upper end of the neck.

To resume, we can regard the cerebro-spinal centres, i.e., the combination of the spinal cord and the brain proper, as being made of nervous matter built round a central opening. This opening runs in the axis of the spinal cord to form what is called the central canal of the cord, whereas in the brain proper, i.e., the portion of the nervous system which is located in the skull, the central opening is no longer a single tube but constitutes the cavities termed the brain ventricles.

In the spinal cord we find the grey nervous matter made almost entirely of nerve cells and occupying the inner part of the cord, while, in the cerebral hemispheres, the grey matter forms a thin layer on the outside surface; this layer is called the brain cortex or simply the cortex. The white matter of the cord, made of bundles of nervous fibres, occupies the outside portion, but in the hemispheres it is inside the cortex, the fibres serving as a link between the various parts of the cortex itself with the cord and with the masses of grey matter located in the lower part of the brain, i.e., in the myelencephalon (or bulb) and the mesencephalon.

Fig. 12 shows a lateral view of the brain in the adult human being. The main point to bear in mind for our

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present purpose is that the true nerve centres are formed by (a) the grey matter of the spinal cord chiefly concerned with the production of reflex movements; (b) a series of masses of grey matter called the basal or primary centres, located in the lower part of the brain (i.e., in or near the bulb), also concerned with the production of reflex action, and governing the work of various organs, apart from the influence of the will; and (c) the grey matter of the cortex which is the centre

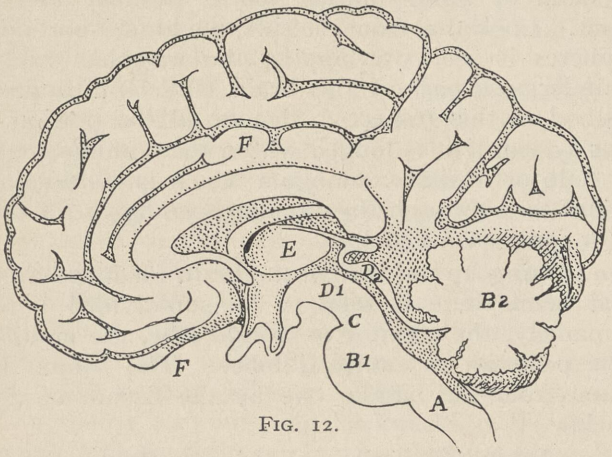


FIG. 12.

FIG. 12. SHOWS A SAGITTAL SECTION OF THE HUMAN BRAIN, PARALLEL TO, BUT NOT COINCIDING WITH, THE MEDIAN PLANE (after His).

(A) is the myelencephalon or bulb.

(B) represents the metencephalon, the front portion (B1) of which is the Pons Varolii, and the back portion (B2) the cerebellum; (C) is the isthmus of the Rhombencephalon; (D) is the mesencephalon, the frontal or ventral portion (D1) of which forms the cerebral peduncles and the back or dorsal portion (D2) develops into the corpora quadrigemina; (E) is the diencephalon including the optic thalamus, the corpora geniculata, the pineal body and the optic tracts; (F) is the telencephalon or end-brain which ultimately forms the cerebral hemispheres.

of voluntary movements and of intellectual functions, as we shall see presently.

The white matter occupying the external part of the spinal cord and the portion of the brain within the cortex is mainly made of fibres arranged in bundles and serving to connect the true nervous centres.

**Description of the Various Parts of the Brain.**

The general scheme of arrangement of the cerebro-spinal centres being understood, it will be well for the student to proceed to a more complete examination of the brain, either on drawings as found in all text-books on Anatomy, or again, on a papier mâché model brain of average size.

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When a human brain is removed from the skull and divested of its sheaths or envelope, or, when a model brain is looked at from above, it shows nothing but the convoluted surfaces of the two hemispheres which constitute the brain proper, the two hemispheres being separated from front to back by a longitudinal fissure. On drawing the two hemispheres apart, they are found to be connected in the middle half, at about 3 or 3.5 cms. below the surface, by a transversal band of white fibrous matter termed the corpus callosum. Looked at from the side, the hinder portion of the hemispheres is seen overlapping the wrinkled cerebellum. The hindermost part of the brain (the term brain being understood in this respect to denote all the portion of the nervous system that is lodged within the cranium) is formed of the bulb or medulla oblongata which is continuous with the spinal cord through the circular opening in the occipital bone (or foramen magnum).

On turning up the base of the brain for inspection, each cerebral hemisphere is seen to be sub-divided into three lobes, namely, the anterior or frontal lobe, the middle lobe, and the posterior or occipital lobe. The frontal lobe is separated from the middle one by the fissure of Sylvius. (See below.)

From behind forwards, in and near the median line of the under surface or base of the brain, the following parts are seen :—

The medulla oblongata, or spinal bulb, or simply the bulb, pyramidal in shape, overlying the cerebellum and with its broad end upwards; certain pairs of the cranial nerves are seen springing from its surface.

The pons Varolii, a quadrate mass immediately above the bulb showing transverse fibres connecting it externally with the two sides of the cerebellum. Internally, it is found to be continuous with the bulb.

The crura cerebri or peduncles of the cerebrum, which show as two striated bundles of nervous matter emerging from the pons Varolii, one on each side of the median line and entering the under part of each cerebral hemisphere as they diverge.

The posterior perforated space, a small triangular plate of brain tissue traversed by many arteries and the corpora albicantia, two small white round bodies each having about the size of a pea, and whose function is unknown. Both the posterior perforated space and the corpora albicantia lie between the diverging peduncles referred to just now.

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The tuber cinereum, an eminence of grey matter in front of the corpora albicantia and attached to the chiasma or optic commissure (the junction of the two optic nerves).

The infundibulum, a hollow conical process passing from the tuber cinereum to a small reddish body of uncertain function called the pituitary body. Being enclosed in the dura mater the pituitary body is usually detached when a brain is removed from the skull and divested of its envelopes.

Lying in grooves on the under surface of the frontal lobes of the brain, on each side of the longitudinal fissure, are the two olfactory tracts and bulbs.

This is about all we can see by mere inspection of a brain. To get an idea of the inner relations of the various parts as well as to see the basal ganglia and cavities of the brain, sections have to be made in various directions. A vertical longitudinal section passing through the middle line of the brain, from front to back, and thus dividing it into two similar and symmetrical halves, will help in the study of the internal structure. We will suppose that we examine the cut surface of the right hemisphere of the brain as exposed by this section. The following structural details may be made out. The corpus callosum is seen cut across; above this and extending forwards and backwards is the flattened exposed surface of the right cerebral hemisphere which forms one side of the median fissure. The upper end of the spinal cord passes into the bulb, in front of which the transversal fibres of the pons are seen in section, while the longitudinal fibres of the bulb run forward above the pons to emerge in front as one of the peduncles of the brain or the crura cerebri (the right one). Anteriorly, the peduncle disappears from the section as it diverges to the right from the median line to enter the corresponding hemisphere. The cerebellum is seen in section overhanging the bulb, and between it and the bulb is the cavity which is called the fourth ventricle. The central canal of the spinal cord opens in the hinder part of the fourth ventricle, while the front end of the cavity is prolonged by a narrow passage (aqueduct of Sylvius) which leads into a longer cavity known as the third ventricle. Above the aqueduct are four masses of grey nervous matter arranged in two pairs, one on each side of the median line of the brain; from their number, these structures have received the name of corpora quadrigemina or quadrigeminal bodies. In front of the anterior quadrigeminal bodies and on the median line is the small structure, about the size of a cherry stone, that is called the pineal gland. The posterior quadrigeminal body on each side is continuous with a thin

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layer of grey nervous tissue which leads back into the cerebellum. This forms an overhanging roof to the front end of the fourth ventricle, and is known as the valve of Vieussens. The floor of the third ventricle is produced forwards and downwards into a funnel-shaped space to the tip of which is attached the small body of glandular nature we have already alluded to under the name of pituitary body. The roof of the third ventricle is provided by a layer of tissue seen in section and known as the fornix. This is connected posteriorly with the hinder end of the corpus callosum and, in front, it curves downwards and backwards into the lateral wall of the third ventricle towards the corpus albicans.

The vertical space between the fornix and the corpus callosum is filled by a thin double layer of nervous tissue called the septum lucidum. It lies in the plane of the section and forms the inner wall of a large cavity occupying the middle of the cerebral hemisphere; this cavity is the (right) lateral ventricle. The lateral ventricle communicates with the cavity of the third ventricle by a small opening termed the foramen of Monro. Since the septum lucidum is made of two layers applied to one another, there is a small flattened space between the two, in the median line of the brain; this is spoken of as the fifth ventricle, but it has no connection with the other cerebral ventricles. The two lateral ventricles, one in each hemisphere, are reckoned as the first and second ventricles; then comes the third and fourth ventricle, each of which is symmetrically placed with respect to the median line. The space between the two layers of the septum lucidum constitutes the fifth ventricle.

Each lateral ventricle is a cavity of peculiar shape, one branch running forwards towards the front end of the hemisphere and one backwards towards the hinder end; from the latter a third branch runs downwards and one more forwards. These branches correspond to the chief lobes of which each hemisphere is made up, namely, the frontal, the parietal and occipital lobes and the temporal lobe. These lobes are marked off on the surface of the hemispheres by fissures, the most conspicuous of which are the fissure of Sylvius and the fissure of Rolando.

We have seen that the spinal cord consists essentially of a central canal surrounded by grey matter containing nerve cells, external to which is a covering of white matter made chiefly of nerve fibres. Now, from what we have learnt just now, it is clear that the brain may also be regarded as being built of structures which are placed round the sides of a central canal which is really the continuation of the central canal of the cord. Only this canal is not a simple

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straight tube but has a peculiar shape. As we have seen, the central canal of the cord is continued upwards by the fourth ventricle which communicates with another central cavity (the third ventricle) by means of the aqueduct of Sylvius. The third ventricle itself is in communication, on the right and on the left, with larger cavities in the cerebral hemispheres, these cavities being the first and second ventricles, or, as they are more often termed, the lateral ventricles. The so-called fifth ventricle is not connected with the other ones.

We have seen just now that at a very early stage of development a folding in of the cells takes place on the dorsal part of the embryo brain, so that the upper area assumes the character of a groove which is termed the medullary or neural groove. As growth proceeds, and the ectodermic cells continue to multiply and to increase in number, the two edges of the groove gradually approximate and ultimately fuse together thus transforming what was the groove into a closed canal, the medullary or neural canal, which is destined to become the central canal of the spinal cord and the ventricles or cavities in the brain. It is from the walls of this canal, which are composed of cells of ectodermic origin, that the brain and spinal cord are formed by cell-multiplication and by outgrowth of existing parts. At first the cells appear all similar, but as the development goes on they begin to differentiate themselves into various kinds, some forming the actual nervous cells and fibres of the brain and spinal cord, others developing into protective structures.

The hinder or posterior part of the medullary canal is narrower than the anterior portion, and gives rise to the spinal cord. It soon changes its character by the appearance of a number of constrictions at intervals running along the whole length; it becomes, as it is termed, segmented, and a little later these successive segments are seen to correspond to the pairs of spinal nerves which arise from the cord.

The front or anterior portion of the medullary canal is concerned with the development of the brain itself, and here, at an early stage, two obvious constrictions occur, and divide the brain area into the three distinct parts or vesicles we have mentioned above. Part of the posterior vesicle ultimately develops into the cerebellum or small brain, while another part forms the spinal bulb or medulla oblongata, that important part of the hind brain in which lie so many centres of nervous energy. The central part formed by these constrictions will ultimately develop into the mid-brain, while



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the foremost or anterior vesicle will form the great mass of the cerebrum itself, together with various outgrowths which have most important functions; two of these outgrowths which appear projecting from the lower part of the sides of the walls and ultimately reach the outer ectoderm of the embryo, are called the optic vesicles, from which the nervous apparatus of the eyes is formed. Later in the development the whole of the anterior cerebral vesicle is again constricted, thus forming two distinct parts, the foremost of which grows rapidly in two halves on either side of the middle line to give rise to the cerebral hemispheres. It follows from this that the two cerebral hemispheres arise in the first place as lateral enlargements of the anterior part of one of the primitive constrictions of the medullary canal. In their outer layers cells continue to develop with great rapidity, and thus is formed the cerebral cortex. According to some authorities, a remarkable thing about this most important part of the brain is that the cells of the cortex appear to be formed during the life of the embryo, there being, in all probability, none added after birth. The consequence of this is that since the cerebral cortex is, as we shall see presently, the centre of all intellectual faculties, then, the capabilities of the brain tissue are fixed from the beginning. In other words, according to these authorities, brain tissue is born and not made, and it is the manner in which it is treated afterwards which determines whether that given amount of brain cells displays its best potentialities or not. However, the fact upon which this theory rests is not definitely proved.

**Arrangement of the Grey Nervous Matter in the Brain.**

Though the brain is, like the spinal cord, made of grey and white matter, these are not arranged in such a simple way as they are in the cord. On the contrary, although in the brain a great deal of grey matter is placed external to the white, the latter is interspersed with localised deposits of grey matter, some small, some large, and this gives to the whole an extraordinary complexity. This complexity is increased by the existence of bundles of nerve fibres which serve to interconnect all these various deposits of grey matter so as to ensure the possibility of co-ordinated action between the individual parts of which the brain as a whole is built.

We cannot undertake to deal with the arrangement of the masses of grey matter in the brain and with their connections by strands or bundles of nerve fibres, but some of these structures are of great importance from our point of view and deserve a brief explanation. We have pointed out the existence of four conspicuous masses of nervous tissue lying

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in two pairs above the aqueduct of Sylvius. They consist of deposits of grey matter in the otherwise thin wall of the roof of the aqueduct. From each of these deposits (or corpora quadrigemina) an arm or a band of fibres runs obliquely downwards and forwards, the arms proceeding from the anterior pair being connected with the optic tracts, while those from the posterior pair serve to make similar connections with the nerves concerned in hearing (acoustic nerves).

We have stated before that the longitudinal fibres of the bulb pass between the transversal fibres of the pons Varolii to reappear as the crura cerebri, or cerebral peduncles, which diverge from the middle line to enter the cerebral hemispheres. As each peduncle passes into the base of the corresponding hemisphere it receives, on its upper surface, a large deposit of grey matter called the optic thalamus. Lying thus to one side of the third ventricle and under the lateral ventricle, each thalamus forms a projection in the outer side wall of the third ventricle and on the floor of the lateral ventricle. The posterior end of each thalamus is called the pulvinar and projects over the arms of the corpora quadrigemina. Two small masses of grey matter termed the geniculate bodies or the corpora geniculata (internal and external) are immediately below the pulvinar, their inner sides forming the lateral boundary of the third ventricle.

The brain is invested by three membranes which are the same in name and are similarly placed and related to each other as those we have described as covering the spinal cord. Of these, the pia mater is highly vascular and carries blood-vessels down into the grey matter, especially into the grooves or sulci to which the convoluted appearance of the surface of the brain is due.

In the spinal bulb the arrangement of the white and grey matter is substantially similar to that which obtains in the spinal cord, i.e., the white matter is external, the grey internal, but the grey matter is more abundant and, as we proceed upwards in the bulb, the arrangement of white and grey matter becomes more intricate and complex.

Above the bulb there are internal deposits of grey matter at various places: we have mentioned the corpora quadrigemina, the optic thalami, the corpora geniculata. What especially characterises the brain is the presence of a particular form of grey matter on the surface of the cerebral hemispheres known as the cerebral cortex. This superficial grey matter covers the whole surface of both the brain proper

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or cerebrum and the cerebellum, dipping down into the fissures or sulci of the former and following the peculiar plaits into which the surface of the latter is thrown.

The surface of the cerebellum presents a corrugated or laminated appearance. When a section is made through one of its hemispheres, it is seen that the depressions which separate the laminæ give off secondary lateral depressions as they pass towards the centre, so that the surface is really divided up into a large number of leaf-like foldings which are known as the lamellæ. The central part of the cerebellum consists of white matter similar to that of the cord, i.e., made of medullated fibres. Portions of this white matter extend outwards into the lamellæ and foldings of the surface, and are partly covered by grey matter, the arrangement thus presenting a peculiar arborescent appearance called arbor vitæ (tree of life) by the earlier anatomists.

**The Cerebral Cortex.**

In the cortex of the brain the grey matter is permeated throughout by neuroglia, or nerve glue, which forms the supporting tissue in which the nerve cells of the cortex are embedded, and through which the nerve fibres pass to and from these cells. The neuroglia is most marked in the outermost parts of the cortex, immediately below the pia mater, and since in a section its wavy fibres are mostly seen as sectional dots, this layer of the cortex is termed the molecular layer. Internally to this is a layer characterised by the presence of nerve cells of pyramidal shape with the apex of each cell pointing towards the surface of the brain. This layer is called the layer of pyramidal cells. The size of the pyramidal cells varies in the different parts of the layer, the largest being found in the inner portion, the smallest near to the molecular layer. Following the layer of pyramidal cells, we find the portion of the cortex which lies immediately external to the central white matter and is characterised by the presence of nerve cells of somewhat irregular form; it is the layer of polymorphous cells.

The white matter of the cerebral hemisphere consists of medullated fibres without their external sheaths, arranged in bundles separated by neuroglia. These bundles may be classified, according to their general course, into (1) diverging or peduncular fibres which connect each hemisphere with the lower portions of the brain and the spinal cord: the fibres of these bundles are in a great measure direct prolongations of the axons of the nerve cells of the cortex; (2) transversal or commissural fibres which include the fibres of the

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corpus callosum and those of the anterior and posterior commissure: they serve to connect the hemispheres; (3) association fibres which connect different structures in the same hemisphere.

**The Functions of the Various Parts of the Brain.**

To complete this brief survey of the nervous system we have to examine the functions of its different parts.

As we have stated before, the spinal cord acts as a large afferent and efferent nerve, as well as a centre for reflex actions.

The spinal bulb, or medulla oblongata, also acts as a conductor, since all the impulses travelling between the brain and the spinal cord must pass through it. Efferent or motor impulses travel mainly through the anterior pyramids which, as already stated, decussate, i.e., cross from one side to the other in the bulb. The path of afferent or sensory impulses is not completely made out, though there is evidence that it is for the most part in the posterior pyramids which also decussate. It follows that all impulses to and from one of the hemispheres of the brain pass across the middle line to the opposite side of the bulb and spinal cord. Any injury of either hemisphere therefore impairs sensations and voluntary movement in the opposite side of the body.

In addition to its function as a conductor of impulses, the bulb acts as a nerve centre, or more exactly, as a collection of nerve centres. The importance of the bulb as a nerve centre is established by the fatal results following its injury or disease. Any sudden displacement of the upper vertebræ of the vertebral column, as occurs in hanging, so injures the cord and its connection as to produce instant death. By experiments on the lower animals it has been proved that the whole of the brain except the bulb may be gradually removed while respiration and life continue for some time.

Most of the nerve centres of the bulb are reflex centres, but the reflex actions under its control are more complicated than those of the spinal cord. Unlike the brain proper, the bulb discharges no mental functions, and initiates none but reflex movements. The bulb contains a respiratory centre, the afferent path of which is the vagus nerve or tenth nerve (see below) distributed to the lungs, and the efferent path, the various motor nerves associated with respiratory movements (phrenic and intercostal nerves). The impulses created by the condition of the blood in the lungs travel by the afferent path to the respiratory centre in the bulb and the consequent motor impulses travel by the efferent path to the muscles associated with the movements of the lungs. There

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are also in the bulb two cardiac centres, a vaso-motor centre (see below), and various other centres for mastication, for deglutition, for salivary secretion, for dilatation of the pupil, etc. Of the two cardiac centres, one serves to accelerate, the other to inhibit, i.e., to slow down, the action of the heart. The vaso-motor centre dominates the nerves supplied to the unstriped muscles of the walls of the arteries. Under ordinary circumstances, it acts continuously or tonically, and keeps the arteries of the body in a state of tonic contraction. Stimulation of the centre leads to contraction of the arteries and to general rise of blood pressure; inhibition of the centre leads to dilatation of the arteries and fall of blood pressure.

**The Cranial Nerves.**

We have mentioned before the thirty-one pairs of spinal nerves which are distributed to the muscles and the skin in all parts of the body. In addition to those nerves there are twelve pairs of cranial or cerebral nerves which appear to rise from the under surface of the brain in a double series and pass through the base of the skull to their ultimate destinations. Their superficial origins, i.e., the points from which they emerge from the under surface of the brain, extend from the lower end of the bulb forwards to the posterior end of the frontal lobe. Their ultimate destination is to some part of the head except in the case of the 10th and 11th. Their fibres, however, can be traced into the substance of the brain to some special masses of grey matter which are termed their deep or real origins, or again, the roots or the nuclei of the nerves. With one exception (that of the first or olfactory nerve) the fibres proceeding from the nuclei of origin cross within the cranium, and the nerves on each side are thus functionally connected with the cerebral cortex of the opposite hemisphere.

The cranial nerves have been numbered according to the order in which they emerge from the base of the brain from before backwards, and are also named according to their function or to the part to which they are distributed. They may be enumerated as follows:—

1st Olfactory.
2nd Optic.
3rd Motor oculi.
4th Trochlear.
5th Trigeminus.
6th Abducens.
7th Facial.
8th Auditory.
9th Glosso-pharyngeal.
10th Pneumogastric or Vagus.
11th Spinal accessory.
12th Hypoglossal.

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The first two pairs differ in their origin and mode of development from all the rest; they are really actual outgrowths or processes of the brain itself which have found their way out of the skull cavity. A glance at the under surface of a brain shows that each olfactory tract emerges from the corresponding hemisphere by three branches which soon unite into a single one; this proceeds forwards and ends in a small ovoid body termed the olfactory bulb. Fine fibres proceed from the under surface of the above structure, and passing out of the cranial cavity through the perforated ethmoid bone, are distributed to the mucous membrane lining the cavities of the nose. The optic nerve is also, strictly speaking, a part of the brain, as we shall see more precisely at a later stage.

The first or *Olfactory,* the second or *Optic,* and the eighth or *Auditory* nerves are nerves of special sensibility, inasmuch as whatever stimulus may be brought to bear on them, they respond by giving rise to a sensation of smell, or to a luminous sensation, or to the sensation of a sound respectively. A branch of the fifth nerve, or *Trigeminus,* supplies the fore part of the mucous membrane of the tongue, and is often spoken of as the gustatory nerve; this branch constitutes also a nerve of special sensibility. Likewise, a branch of the ninth pair is distributed to the hind part of the mucous membrane of the tongue and is also concerned with the sense of taste.

Of the other cranial nerves, some are motor nerves, some are sensory, and some are mixed, i.e., sensory and motor. The purely motor nerves are: the 3rd or *Motor oculi,* the 4th or *Trochlear,* the 5th or *Trigeminus* (except for the branch which constitutes the gustatory nerve and those supplying sensibility to the conjunctiva, the face, etc.), the 6th or *Abducens,* the 7th or *Facial,* and the 12th or *Hypoglossal.* The mixed nerves are the 9th or *Glosso-pharyngeal* (with the exception of the branch of special sensibility referred to above), the 10th or *Vagus* or *Pneumogastric,* and the 11th or *Spinal accessory.*

We have already pointed out that the olfactory nerves are really lobes of the brain, and arise by a triple root in the under part of the front lobe. The two olfactory tracts lie in a furrow on either side of the median fissure of the brain, and each one terminates in an ovoid bulb, from the under surface of which ten or twelve fibres (or true olfactory nerves) pass through the cribriform plate of the ethmoid bone and are distributed to the mucous membrane of the nose, there forming the terminal or peripheral organ of the sense of

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smell. Unlike all other nerves, the sensory impressions do not cross to the opposite side of the brain.

The arrangement of the second or optic nerve will be examined in detail later on. For the present it is sufficient to say that the two optic nerves are connected together at the chiasma or optic commissure, where a partial decussation takes place. Behind the chiasma, under the name of optic tracts, the optic nerves may be traced to their origin in the anterior quadrigeminal bodies and the external geniculate bodies. From these nuclei of origin, fibres (constituting the optic radiation) may be traced to the visual centre in the cortex of the occipital lobe.

The nerves of the third pair or *Motor oculi* have their origin in clusters of cells in the grey matter of the cerebral peduncles on each side of the aqueduct of Sylvius, where the nerves of the two sides decussate. The 3rd nerve is purely motor or efferent, and passes by two main branches into the orbit. There these two main branches divide to be distributed (1) to the levator of the upper lid; (2) to the superior rectus; (3) to the inferior rectus; (4) to the internal rectus; (5) to the inferior oblique; (6) to the ciliary muscle; and (7) to the sphincter of the iris.

The fourth or *Trochlear* nerve arises from a nucleus of large cells immediately below the nucleus of the third nerve in the floor of the aqueduct. It is purely motor and supplies the trochlear or superior oblique muscle.

The fifth or *Trigeminus* has two superficial origins, or two roots, like a spinal nerve, a larger sensory root in connection with a ganglion termed Gasser's ganglion, and a smaller motor root without a ganglion. Its nuclei are in the portion of the pons which forms the floor of the fourth ventricle. The sensory part of the nerve is distributed to the face, the teeth, the mucous membranes of the nose and mouth, and to the eye, as we shall see later on. The motor part of the 5th nerve passes mainly to the muscles serving for mastication and to the muscles of the palate. A branch of the 5th nerve termed the Chorda Tympani, though efferent, does not supply muscles, but is distributed to the salivary glands and stimulation of this branch causes an increased flow of saliva.

The sixth or *Abducens* nerve arises from a nucleus in the pons, above the middle of the floor of the fourth ventricle. It is exclusively motor, and supplies only the external rectus muscle.

The seventh or *Facial* nerve arises from a nucleus in the pons, near that of the sixth, and supplies all the muscles of

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facial expression; its paralysis or injury leads to one side of the face having a blank look, while the angle of the mouth on the same side droops.

The other cranial nerves, i.e., the 8th or *Auditory,* the 9th or *Glosso-pharyngeal,* the 10th or *Pneumogastric,* the 11th or *Spinal accessory,* and the 12th or *Hypoglossal,* are not concerned with the working of the eye, and we will not say any more about them except that the auditory nerve serves to the perception of sounds, i.e., is a purely sensorial nerve. The 10th or pneumogastric or vagus nerve supplies the larynx, the lungs, the liver, the stomach, and branches of it are distributed to the heart. It is both sensory and motor, carrying efferent impulses to the muscles of the above-named organs, and inhibitory impulses to the heart. Amongst its afferent fibres, some convey to the nervous centres those impulses from the respiratory and digestive organs which lead to the phenomena of coughing and vomiting. Section of both pneumogastric nerves in the neck leads to acceleration of the heart beats, difficulty in swallowing owing to paralysis of the muscles of the pharynx, slow but deeper respiration due to paralysis of the muscles of the larynx. In such cases foreign particles accumulate in the insensitive larynx and air passages, and may ultimately give rise to a fatal inflammation of the lungs. The pneumogastric nerve is the only cranial nerve which supplies parts of the body outside the head.

The 11th and 12th pairs, i.e., the spinal accessory and the hypoglossal, are purely motor and supply, the former some of the muscles of the neck, the latter the muscles of the tongue, and those muscles connected with the hyoid bone.

**Functions of the Cerebellum.**

The functions of the cerebellum or small brain appear to be concerned with a proper co-ordination of the various movements of the body and to insure that in any action, such as standing or walking, the different muscles employed may each act at the right moment and with the proper degree of force. The fact is shown by the behaviour of an animal in which the cerebellum has been removed. The animal does not differ in any essential respect from its normal condition as regards intelligence and special senses, such as sight or hearing, but with regard to its movements, a great difference is obvious; all movements are clumsily performed, and there is a total lack of orderliness or co-ordination.

It should be observed that the work of muscular co-ordination is not entirely due to the cerebellum. For

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instance, the auditory nerve (8th cranial nerve) consists of two distinct parts, namely, the true auditory nerve which is concerned with the perception of sounds, and another branch, often called the vestibular branch which is distributed to the semi-circular canals of the internal ear. The 8th nerve originates from a nucleus of grey matter in the bulb and the portion of this nucleus which gives rise to the vestibular branch of the 8th nerve is connected by a strand of fibres with the cerebellum. Thus, there is a path by which afferent or sensory impulses from the semi-circular canals may directly reach the cerebellum, and there be turned to account in the co-ordination of movements. It is not surprising, therefore, to find that the semi-circular canals, whatever part they may play in hearing, play an important part in the co-ordination of movements. Other afferent impulses which contribute to the co-ordination of movements are muscular sensations which form the basis of the muscular sense, and visual sensations, as we shall see presently.

We have stated just now that removal or injury of the cerebellum causes a want of co-ordination of movements. If one side only is removed or injured, there is an inclination to fall towards the opposite side through failure of muscular power on the injured side. It can be further ascertained that excitation of one side of the cerebellum gives rise to muscular contraction on the same side of the body. Moreover, dissection and the observation of the path of degeneration show that the connection of the cerebellar hemispheres with the cerebral hemispheres is crossed. Finally, disease of the cerebellum generally leads to a staggering gait with loss of muscular power and tone. These facts enable us to conclude that each cerebellar hemisphere is connected with the same side of the body but with the opposite hemisphere of the brain, and that the main function of the cerebellum is to insure co-ordination of muscular movements, and to maintain muscular energy. It does not share in the higher intellectual functions, since its destruction does not affect the mental faculties.

**Functions of the Cerebral Hemispheres.**

The functions of the parts of the brain which lie in front of the bulb (brain proper) may be inferred from the fact that extensive injury or removal of the cerebral hemispheres puts an end to intelligence and voluntary movements, and leaves the animal in the condition of a machine working by the reflex actions of the remainder of the cerebro-spinal system. We have pointed out that in the frog the movements of the body which the cord alone, in the absence of the whole of

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the brain, is capable of performing, are complex and varied, but none of these movements arises from changes originating in the organism; they are not voluntary or spontaneous movements, and do not occur unless the animal is stimulated from without. Removal of the cerebral hemispheres is alone sufficient to deprive the frog from all voluntary or spontaneous movements; the presence of the bulb and the cerebellum renders the frog master of movements of a higher nature than when the cord only is left. In the latter case the animal does not breathe when left to itself, it lies flat, and, when irritated, it kicks out its legs but never jumps from place to place. When thrown in water, it sinks to the bottom, and if placed on its back it remains so and makes no attempt to turn over. In the former case, the animal sits in its natural position, breathes quite naturally, and jumps if stimulated. When thrown into water, it swims until it meets an obstacle and turns over if placed on its back. Though all these movements, when they occur, are well combined and apparently identical to those performed by a normal frog, yet they are never performed spontaneously; the animal does not stir unless irritated.

Thus, the parts of the brain below the cerebral hemispheres constitute a complex nervous machinery for carrying out intricate and orderly movements in which afferent impulses play an important part, but they do not give rise to changes of consciousness. The cerebral hemispheres are the seat of powers essential to the production of those phenomena we term intelligence and will. There is evidence to indicate a connection between particular parts of the surface of the cerebral hemispheres and particular acts; thus, irritation of a particular spot in the anterior part of a dog's brain gives rise to particular movements of this or that limb; destruction or injury of a certain part of the posterior lobes of the hemispheres leads to blindness. The exact way in which these effects are brought about is not yet thoroughly understood, and though we have learnt much on the subject in recent years, we are still in the dark as to what goes on in the cerebral hemispheres when we think or when we exert our will. There is no doubt that a molecular change in some parts of the cerebral substance is an indispensable antecedent to every phenomenon of consciousness, and it is possible that future progress in physiologic science will enable us to map out the brain according to the psychical relations of its different parts, but, assuming we get so far as to be able to prove that the irritation of a particular fragment of cerebral substance gives rise to a particular state of consciousness,

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this will not explain the reason of the connection between the molecular disturbance and the psychical phenomenon.

**Nervous Energy and its Correlation with other Forms of Energy.**

As we have pointed out before, it is now well proved that most of the phenomena concerned with the nutrition of the living body are explainable by means of the laws of physics and chemistry, and are dependent upon the fundamental laws, namely, the law of conservation of energy and the law of indestructibility of matter which form the keystone of natural science. The principal categories of physiological action, e.g., Digestion, Assimilation, Circulation, Respiration, are readily understood as being controlled by the action of physical and chemical forces. When, however, we come to try to apply physico-chemical principles to the work of the nervous system, we meet with what seems at first an insuperable difficulty. When dealing with the grosser question of chemical compounds, heat and motion, we find it easy to apply natural laws to the explanation of phenomena in the living body, but the problem is very different in the case of the nervous system. It is true that mental and other nervous phenomena have been studied for a long time by psychologists, but this study has been simply the study of these phenomena by themselves without a thought of their correlation with other phenomena of nature. It is only recently that the conception that nervous phenomena have a direct relation to the physico-chemical laws has been advanced. The first question which has to be answered is whether we can find any correlation between nervous energy and other types of energy. For our purpose it will be convenient to distinguish between the phenomena of simple nervous transmission and the phenomena of mental activity. The former are the simpler and offer the greatest hope of solution. That there is a correlation between nervous energy and physical energy is fairly definitely proved by experiments on different lines.

The first step was to find that a nervous stimulus can be measured at least indirectly. Where a nerve is stimulated there passes along it an impulse, the speed of propagation of which can be accurately measured, as we have seen in page 52. When the impulse reaches the brain, it may give rise to a conscious sensation, and a somewhat definite estimation of the time required for this can be made. The periods are very short, of course, but are not instantaneous. In fact, mental operations take a longer period than simple reflex actions. By means of suitable apparatus, a system of signalling and a method of recording extremely short periods

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of time with tuning forks worked by an electric current, the time it takes for a cerebral operation can be measured with a fair degree of accuracy. A stimulus is applied to a nerve, e.g., the optic nerve or the acoustic nerve, by means of, say, an induction coil. The subject experimented upon gives a signal the instant he perceives a sensation of light or of sound, both the exact time of application of the stimulus and the time of the signal given by the subject being recorded on a revolving drum on which the vibrations of the tuning fork are also registered. The interval between the instant the stimulus is applied and the instant a sensation results and is recorded, is termed the reaction period. This period obviously includes the time taken by the impulse due to the stimulus to travel from the point of application of the stimulus to the nervous cortical centre along the nerve concerned, the perception by the mind and the time occupied by the motor impulse to travel from the cortex to the muscle concerned in signalling the receipt of the sensory impulse.

The reaction period for hearing is 1-6th of a second, for sight 1-5th of a second, for feeling a mechanical stimulus applied to the skin 1-7th of a second. These figures vary, however, in different individuals.

The nervous impulses can be studied in other ways. We know that such impulses can be started by ordinary forms of energy. A mechanical shock or a chemical one, or an electrical one will give rise to nervous energy. Now, these are ordinary forms of energy, and since, when applied to a nerve, they give rise to a nervous impulse, it is logical to infer that the nerve is a bit of machinery adapted to the conversion of certain kinds of physical energy into nervous energy. Other facts point to the same conclusion. Not only can the nervous stimulus be developed by an electric shock, but the strength of the stimulus is, to a certain extent, proportional to the strength of the shock which produces it. Again, not only is it found that an electric shock can develop a nervous stimulus, but conversely a nervous stimulus develops an electric current. In a nerve at rest slight electric currents can be detected; these currents are very weak, and can only be ascertained by most accurate instruments. Now, when a nerve is stimulated, i.e., is at work, these currents are affected in such a way that they increase in intensity and become sufficient to act on a sensitive galvanometer. These facts prove clearly that nervous energy is correlated with other forms of physical energy. Since a nervous stimulus is started by other forms of energy, and since it can in turn modify ordinary forms of energy, we arrive at the conclusion that the nervous impulse is only a special form of energy

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developed within the nerve. A nervous impulse is thus a form of molecular disturbance, a form of wave motion peculiar to the nerve substance, but correlated with and developed from other types of energy.

As to the activities of nerve cells, little is known at present. It has been found that certain visible changes occur in the brain cells when they are excited into mental activities. We shall see later on that the protoplasm of nervous cells contains granules of matter (*Nissl's granules*) which are used up when the cell is active and become re-formed in the periods of rest. This fact, to which we shall refer again in the study of the retina, seems to imply an association between the mental side of sensation and the physical structure of the nervous centres. It does not, however, prove a correlation between the two, and in the present state of science, the unlikeness of mental and physical phenomena is so absolute that we must hesitate about drawing any connection between them.

Chemical substances of a proteid nature and rich in phosphorous compounds, abound in the protoplasm of a nervous cell, and the activity of the nervous protoplasm depends more on an ample supply of oxygen and the removal of waste matter than that of any other kind of protoplasm. It is doubtful whether the protoplasm of a neuron, say, in the brain, can act for longer than a few seconds without oxygen being supplied to it, and the waste product removed. Hence, there is immediate loss of consciousness if the supply of blood is cut off from the brain, and if the quality of the blood is altered by the presence of even small amounts of poison, the effect is quickly felt.

Nervous matter is also extremely sensitive to shocks or variations of pressure. Thus a sudden concussion will often produce unconsciousness. The activities of the nervous system, and especially the mental activities depend on the interplay between grey matter and blood, and the limit of adaptation as regards blood supply, quality of blood and temperature is very small. In fact, nearly all the other functions of the body are in a sense working towards the end of the adequate nutrition of the grey cerebral matter.

Even when the cerebral hemispheres are entire and in full possession of their powers, the brain gives rise to actions which are as completely reflex as those of the spinal cord. When the lids wink at a flash of light or at a threatened blow, a reflex action takes place, in which the afferent path is the optic nerve, the efferent the motor oculi. When the pupil contracts on illumination of the eye, we have again a reflex action, the afferent and efferent paths of which are

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the same as before. In those cases, the reflex action produced must be effected through the brain, since all the nerves concerned are cerebral nerves. When the whole body starts at a sudden and loud noise, the afferent auditory nerves give rise to an impulse which passes to the bulb, and then through the spinal cord, affects the majority of the motor nerves of the body.

It may be objected that these are mere mechanical actions having nothing to do with the operations we associate with intelligence. But let us consider a more complex act, for instance, that of reading aloud. In such a case, the whole attention of the mind is, or should be, bent upon the subject of the book, while a number of delicate muscular actions are going on without the reader being aware of them. The book is held at the right distance, the eyes are moved over the lines and up and down the pages, the most delicately adjusted and rapid movement of the muscles of the lips, the tongue, the throat and the respiratory muscles are involved in the production of speech. Perhaps the reader is standing up and accompanies his lecture with appropriate gestures. Yet all these muscular acts are performed with utter unconsciousness on his part of anything but the sense of the words in the book. In other words, they are reflex actions. Similar remarks apply to the act of playing at sight, or from memory, a difficult piece of music.

**Reflex Actions of the Brain.**

The reflex actions proper to the spinal cord are natural and are involved in the structure of the cord and the properties of its constituents. By the help of the brain, we may acquire an infinity of artificial reflex actions, i.e., of actions which may, at first, require all our attention and volition, but which by frequent repetition become, so to speak, part of our organisation, and may be performed without volition or even without consciousness.

Walking is a complex act requiring a long study on the part of the young child, but it ultimately becomes a reflex act; we can walk while reading or speaking. As everybody knows, it takes a long time for a soldier to learn his drill, for instance, to put himself in the attitude of "attention" the instant the word of command is given. After a time the sound of the word is enough to give rise to the act itself whether the soldier thinks of it or not. The drill is intended to embody certain acts in the man's nervous structure, and the possibility of all education is based upon this power the nervous system possesses of organising conscious actions into more or less unconscious or reflex operations.

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It may be laid down as a general rule which is called the law of association, that if any two mental states be called up together or in succession with due frequency, the subsequent production of the one of them is sufficient to call up the other, whether the individual concerned desires it or not. The object of intellectual education is to create such indissoluble association of our ideas of things in the order and rotation in which they occur in nature; that of moral education is to unite the ideas of wicked deeds with those of degradation and pain, and of good actions with those of nobleness and pleasure.

**Phenomena Observed after the Removal of the Cerebral Hemispheres.**

We have alluded to the facts derived from observation of the brainless frog, and have seen that the frog does not move without some external stimulus being applied: all voluntary action has departed and the animal, if left to itself, will sit still till it dies from starvation.

Fishes exhibit similar phenomena; they swim about in the water, but these movements are not voluntary, and result from the stimulus of the water in contact with the body.

A pigeon with the cerebral hemispheres removed sits on its perch and balances itself perfectly. When thrown in the air it flies; when pinched it moves forwards. If not interfered with, it appears to be in a profound sleep, though occasionally it will preen its feathers or yawn. Its pupils contract normally, and it resists any effort made to open its beak, but it swallows when food is placed in its mouth. It performs no spontaneous movement, the yawning and the preening of feathers being probably reflex actions due to the irritation of the wound.

When the cerebral hemispheres of a rabbit are removed, the animal is at first prostrate; after a while it can use its legs, though the fore ones are weak; if pinched, it springs forwards but, unlike the brainless frog, it strikes itself blindly against any obstacle in its path. When pinched severely, it utters cries.

In higher animals, motor paralysis is so marked after the removal of the hemispheres that no definite conclusions concerning equilibrium and co-ordinated movements are possible. At first sight, it would appear that consciousness is necessary for the performance of complicated movements and the avoidance of obstacles on the path of a brainless animal; the cries elicited by pinching would appear to indicate a sensation of pain. Yet a careful study of these phenomena has shown that they are the result of a reflex mechanism and are similar to walking during sleep or to the cries elicited

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from a patient under chloroform. The bulb contains reflex centres for still more complex acts, as, for instance, the reflex expression of emotions, the avoidance of obstacles when leaping, or the co-ordination of other habitual movements.

The result of the experiments on animals described just now are in agreement with what has been observed in the case of a child born without a brain, and who lived three years and nine months. His cerebral hemispheres were reduced to a thin membrane with a double wall in which nervous cells and fibres were entirely absent. All the rest of the cerebro-spinal system was normal except that the cerebellum was somewhat smaller than that of a healthy newborn child. During the first years of his life, the child was immobile in his cot; he never cried and never showed any desire for food, and slept practically all the time. Every three hours he was wakened and was given some milk. He seemed to be deaf, blind and devoid of sensibility generally. At the end of the first year, the only change observed was that the child cried frequently, a fact probably connected with the development of the bulb, but at no time did the subject exhibit any psychical faculty.

**Cerebral Localisation.**

We have mentioned before that there is a connection between particular parts of the surface of the cerebral hemispheres and particular acts or special sensations. The possibility thus indicated is of extreme importance.

The cerebral hemispheres are separated along the middle line of the brain by a narrow deep fissure across which the corpus callosum passes as a bridge. The surface of each hemisphere is folded into a number of convolutions or gyri separated from each other by depressions or sulci. Some of these depressions are deeper than others and are known as fissures. Of these, the most conspicuous are the fissure of Sylvius, the fissure of Rolando, the parieto-occipital fissure and the calcarine fissure, which may be taken as roughly dividing the surface of the hemisphere into several lobes, namely, the frontal, the parietal, the occipital, and the temporal. (See figs. 13 and 14.)

When the surface of a cerebral hemisphere is stimulated, electrically or otherwise, close to the fissure of Rolando, and on either side of this fissure, very definite movements take place in the limbs of the opposite side of the body. If care is taken to localise the stimulation to a small area of the cortex, the resulting movements are found to be restricted to a correspondingly small group of muscles in the affected



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limb. Again, if the piece of cortex whose stimulation gives rise to certain movements be cut out, the animal so operated upon is found to have lost the power of executing these particular movements. The outcome of these experiments makes it clear that the cerebral cortex along the course of the fissure of Rolando is concerned in the production of

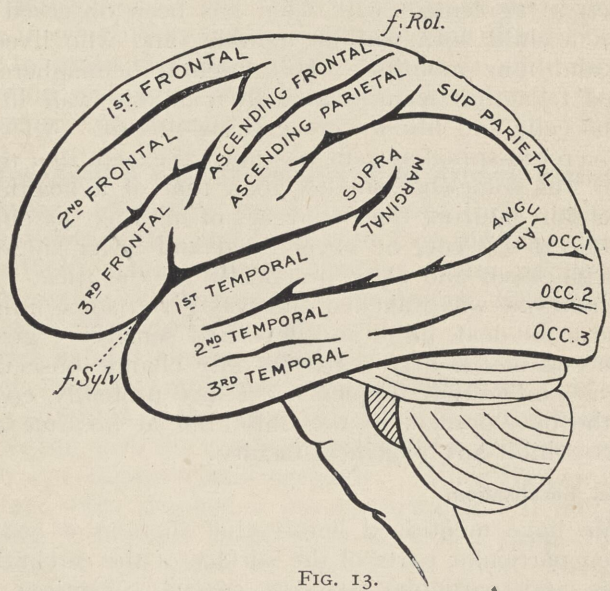


FIG. 13.

FIG. 13. LATERAL OR OUTER ASPECT OF THE LEFT CEREBRAL HEMISPHERE (after Exner).

The surface of each hemisphere presents a peculiar folded appearance, due to the fact that it is thrown into a large number of convolutions (or gyri) separated from each other by sinuous depressions, some of which are deep and well marked and are called fissures, while others, shallower, are termed sulci.

The most conspicuous fissures visible on the outer surface of the hemisphere are the fissure of Rolando and the fissure of Sylvius, which may be regarded as dividing the brain surface into several more or less distinctly marked lobes, namely the frontal, the parietal, the temporal and the occipital lobes. The fissure of Rolando begins near the middle of the great median longitudinal fissure at the vertex and passes on the outer surface of each hemisphere obliquely downwards and forwards. The fissure of Sylvius begins on the under surface of the hemisphere and passes slightly upwards and backwards. The frontal lobe of the brain, subdivided into various convolutions by smaller fissures, lies in front of the fissure of Rolando and above the fissure of Sylvius. The parietal lobe is limited in front by the fissure of Rolando and beneath by the extreme end of the fissure of Sylvius. The temporal lobe lies below the fissure of Sylvius and is separated from the occipital lobe by the almost perpendicular parieto-occipital fissure (not shown on the diagram but visible in FIG. 14). The occipital lobe, which is small and lies at the posterior and inferior part of the brain immediately above the cerebellum, shows on the outer surface of the hemisphere three convolutions, separated from each other by small horizontal sulci, and termed the first, the second and the third occipital convolution.

The calcarine fissure does not show on the outer surface of the cerebral hemisphere, but is seen on the inner surface (see FIG. 14).

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muscular movements of the limbs; hence this portion of the cortex is called a motor area. Further, special movements are associated with particular spots in this region; thus, stimulation of the upper part around the Rolando fissure is associated with movements of the leg; of the middle part, with movements of the arm; of the lower part, with movements of the face. A particular interest attaches to the third frontal convolution on the left side, as a lesion in this part is always associated with the loss of power of speech or *motor aphasia*, as it is called. This part is the same as, or is close to, the motor centre for the muscles of the tongue and mouth, and is known as the speech centre. In right-handed people, the delicate co-ordinated movements of speech are regulated from that particular part of the left hemisphere, the corresponding part of the right hemisphere remaining dormant and uneducated for this work. When this portion of the brain is the seat of injury, there is a total loss of voluntary speech. There is no loss of voice, for the subject can laugh and cry, and even sing, but either he is unable to utter any words at all or he uses wrong ones,

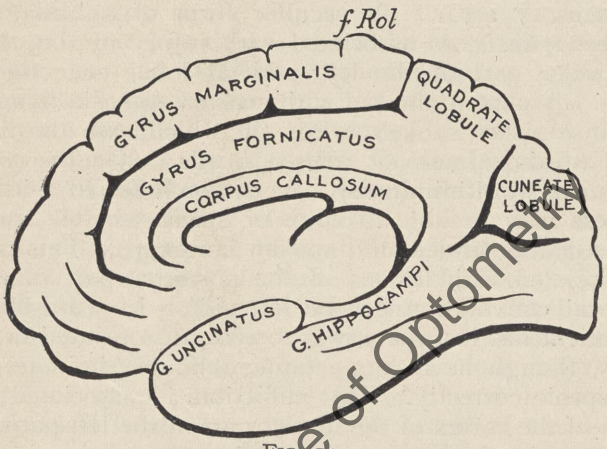


FIG. 14.

FIG. 14. MESIAL ASPECT OF THE RIGHT HEMISPHERE (after Exner). The diagram shows a long fissure, beginning below and running backwards some distance above the corpus callosum, to terminate behind the upper end of Rolando's fissure. This is called the calloso-marginal fissure; between it and the surface of the hemisphere is the marginal convolution (or gyrus marginalis). Between the calloso-marginal fissure and the corpus callosum is the callosal convolution or gyrus fornicatus. The posterior end of the callosal convolution turns downwards and then forwards under the name of hippocampal convolution (gyrus hippocampi). Between the posterior end of the calloso-marginal fissure and the parieto-occipital fissure is the quadrate lobule, while below this, and between the parieto-occipital fissure and the calcarine fissure, is the wedge-shaped mass called the cuneate lobule or cuneus. The part of the cortex immediately above and below the calcarine fissure constitutes the cortical centre for vision.

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speaking incoherently and unintelligibly. He may recognise his mistakes but cannot avoid them. In this motor aphasia the power of writing is often, though not always, lost, as most people silently articulate the words as they write.

Our knowledge of the existence and position of motor areas as derived from experiments on animals is completely confirmed by the anatomo-clinical method, i.e., by an examination after death of the brains of persons who during life had exhibited symptoms similar to those obtainable by stimulation or extirpation of cortical areas in animals.

Proceeding in a similar way, it has been further found that certain portions of the cerebral cortex are peculiarly concerned with the development of sensations. These portions are termed *sensory areas,* and, in their case, observations on man are especially instructive since the subject can give an account of his sensations, whereas animals cannot.

We have pointed out that the cortical centre for vision is in the posterior part of the occipital lobe: this portion of the cortex, which we shall define more precisely later on, is a sensory area. A peculiar form of aphasia, termed *sensory aphasia,* is associated with injury of the cortex of the hinder part of the left parietal lobe, near the visual centre. A person affected with sensory aphasia is unable to recognise either spoken words (in which case the defect is called word-deafness) or written words (when the condition is termed word-blindness). A person affected with word-deafness may be able to write or speak sensible sentences, but he cannot understand spoken language. This affliction is associated with lesions of the posterior part of the first temporal convolution on the left side. In word-blindness, the patient has lost the power to recognise printed or written words, though he may see quite well, discriminate objects, and speak correctly. This affliction is associated with a lesion of the cortex of the hinder part of the left parietal lobe near the visual centre. We shall revert to this interesting side of our subject in the part of this work devoted to the nervous apparatus of vision.

To sum up, the cerebral hemispheres, especially the grey matter of the cortex, are the seat of consciousness, memory, intelligence, and volition. The thickness of the cortex varies between 2 and 4 mms., and the convoluted arrangement of the brain surface is evidently intended to increase the cortical area; this is proved by the fact that the convolutions are less marked in the higher monkeys, still less in other mammals, while the cerebral hemispheres are practically free from convolutions in the lower vertebrates.

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**Relation Between the Size of the Brain and the Intellectual Faculties.**

Since the brain is the seat of psychical and intellectual functions, there must be some relation between the degree of intelligence and the degree of development of the cerebral hemispheres. Observation shows that the cerebral mass is quantitatively in proportion to the intellectual faculties. This conclusion is justified by the figures of the following table established by Leuret, a distinguished mental specialist of French nationality. Taking the weight of the brain as unity, the average total weight of the body is:—

| | |
|---|---|
| In fishes ... ... ... | 5,668 |
| In reptiles ... ... | 1,321 |
| In birds ... ... ... | 212 |
| In mammals ... ... | 106 |
| In man ... ... ... | 35 |

The weight of the cerebrum of the average human being of the white race is 1,300 to 1,360 grammes (i.e., 46 to 48 oz.) out of which about 1,200 grammes (or 42 oz.) represent the weight of the brain proper or cerebral hemispheres. In subjects belonging to the negro race, the weight is usually 70 to 80 grammes less than in the white race. Besides, most of the men of high intellectual powers have a large brain. Well-known instances are those of the anatomist Broca, whose brain weighed 1,484 grammes, of the poet Schiller (1,785 grammes), of the naturalist Cuvier (1,830 grammes). The brain of Lord Byron is said to have had a weight of 2,230 grammes, but this figure is doubtful. There are, however, many exceptions; men of high abilities, with a brain somewhat below the average; in those cases, the brain was found to be exceedingly rich in convolutions. To conclude, it is impossible to ascertain the degree of intelligence in terms of the mere weight of the brain, and the reason for this is that while a great part of the cerebral mass is concerned with psychical functions, a part, the extent of which is not known very exactly, is undoubtedly related to purely corporal functions. However, any subject belonging to the white race whose brain weighs less than 1,000 grammes, can be classified as a mentally defective individual or an idiot. Observations by the anatomo-clinical method have shown that the reduction of the cerebral substance in micro-ancephalia or microcephalia is always accompanied by a proportional loss of intellectual function.

It should be borne in mind that only lesions of the cerebral hemispheres are followed by mental troubles; a lesion of the bulb or the cerebellum does not affect the intellectual faculties.

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From what is said up to now, it is clear that, viewed broadly, the brain is a mass of white matter with various nuclei or ganglia of grey matter deeply embedded into it, and with a sheet of grey matter, about one-fifth of a square metre in area, and between 2 and 4 mms. thick, covering the folds, fissures and convolutions of its surface. This superficial grey matter or cortex is the brain proper, i.e., the organ of sensation, judgment and will. The white matter beneath the cortex is made of fibres leading into it sensory impulses and leading off from it motor impulses; this white matter is merely a conducting mass composed of bundles of medullated nerve fibres disposed in a fan-like manner between the grey matter of the cortex and the region of the base of the brain proper. This mass of white matter is known as the corona radiata. At the base of the brain it forms a conical sheet of white matter which is termed the internal capsule, which constitutes the main channel of motor and sensory impulses. The internal capsule is continued as the two cerebral peduncles (or crura cerebri) which traverse the pons and are continuous with the white columns of the bulb and spinal cord. This main channel gives and takes fibres to and from the ganglionic masses of the base of the brain, which it skirts or traverses, but a large portion of the fibres which constitute it passes directly, as a system of afferent and efferent channels between the grey matter of the cortex and the grey matter of the cord. This is clearly shown by the tract of degeneration that has been traced from the cortex through the corona radiata, internal capsule, cerebral peduncles, anterior pyramids of the bulb to the lateral column of white matter in the opposite side of the cord (the crossed pyramidal tract), and to the anterior column of the same side (direct pyramidal tract). A more detailed account of the connection of the retina with the primary visual centres, and of the primary centres with the cerebral cortex will be given in one of the next chapters.

**Sympathetic Nervous System.**

The portion of the nervous system we have studied so far is known as the cerebro-spinal system. We have alluded before to the sympathetic system and have pointed out that it is not a separate system, its ganglia being in connection with fibres proceeding from the posterior root of the spinal nerves, and that its nerves are under the control of some parts of the cerebro-spinal system. From the ganglia of the sympathetic system fibres pass to all internal viscera as well as to the walls of the arteries.

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The sympathetic system exercises an influence over the greater part of the internal machinery and, to a certain extent, it controls the functions of digestion, nutrition, circulation, respiration, etc. A most important function of the sympathetic system is the control it exerts on the blood-vessels. We have seen that the walls of the arteries contain muscular fibres of the smooth or involuntary variety. These fibres become relatively more abundant as the arteries become smaller. The working of these muscular fibres is not under the influence of the will; we cannot make up our mind to regulate the flow of blood through the arteries and then carry out our wish. These vessels are controlled by the sympathetic nerves which perform their duties by a sort of reflex action. Under the influence of these nerves the muscles in the walls of the arteries are caused to contract, and then the vessels themselves become smaller and the flow of blood in them is retarded. In ordinary conditions, the arteries are kept in a state of moderate contraction or tone by a slight nervous discharge originating constantly from a portion of the upper part of the spinal cord which is termed a vaso-motor centre. Fibres from that centre pass along the posterior root to a sympathetic ganglion and then to the arterial walls.

Blushing is explained in this way. Certain emotions first spring in the mind, i.e., in the cerebral cortex; their influence is extended through the bulb to the vaso-motor centre in the spinal cord; the activity of this centre diminishes, with the result that the muscles in the arterial vessels relax, the blood-vessels then become larger, the flux of blood is increased, a hot flush is felt, and the skin grows red. According to the intensity of the original emotion, these changes are localised to the cheeks only, or extend to the roots of the hair, or all over. Other emotions, e.g., extreme terror, anger, cause the skin to grow cold and the face to appear pale and pinched; under these circumstances, the supply of blood to the skin is greatly diminished in consequence of an increased contraction of the muscles in the walls of the smaller arteries whereby these become unduly constricted and allow only a smaller amount of blood to flow through them. Sudden paleness is perhaps more often due to a failure of the heart's beat, as in fainting, but it may also occur, as stated just now, when there is no change in the beat of the heart.

The above remarks show plainly the importance of the sympathetic nerves for the regulation of the blood supply generally. If the arterial walls had no tone they would, under ordinary resting conditions, be dilated to their full

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extent, and the part they supply with blood would receive a maximum supply when at rest. But the organs of the body are never at rest for long, and when they become active they require an increased amount of blood. This could, of course, be done by an increased activity of the heart, but then the whole body would receive an excessive supply, while what is really wanted is a localised variation in supply to meet the varying needs of each part or organ. The purpose of the vaso-motor nerves is precisely to regulate the blood supply of each part or organ, according to its state of activity or of rest. The vaso-motor nerves act by carrying more or less of the same kind of impulse, leading to an increase or a loss of tone and hence to a lessened or an increased blood supply.

We have quoted blushing as being a characteristic and familiar instance of the action of the vaso-motor nerves. Similar instances are met with throughout the whole body. Thus, when a muscle contracts, or a salivary gland secretes saliva, or the lachrymal gland secretes tears, or when the stomach is preparing to digest food, in each case the small arteries of the muscle, the glands or stomach dilate and flush the part with blood. The organ, in fact, blushes and this inner, unseen blushing, like ordinary blushing, is brought about by the action of the vaso-motor nerves. The temperature of the body is largely regulated by the supply of blood to the skin, and this supply is, in its turn, regulated by the vaso-motor nerves. Indeed, everywhere the nervous system by its vaso-motor nerves is regulating the supply of blood, sending now more and now less blood to this or that part, and many diseases, such as those in which exposure to cold causes congestion or inflammation, are due to, or at least, associated with, a disorder or a failure of this vaso-motor activity.

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## CHAPTER V.

### LIVING TISSUES—*(Continued)*. NUTRIENT TISSUES. NUTRITION OF THE BODY GENERALLY. ANIMAL HEAT.

**The Blood and the Nutrient Tissues Generally.**

It may appear strange to describe the blood as a tissue, yet the description is quite justified by the fact that the blood is really made of solid particles, the blood corpuscles, in suspension in a nearly colourless fluid, the plasma. The blood is therefore comparable to a connective tissue, the matrix or intercellular part of which is represented by the plasma, holding in suspension an immense number of solid particles we have already alluded to as blood corpuscles. The plasma consists of 90 per cent. of water and 10 per cent. of solid matter dissolved in it, this solid matter being chiefly proteids with a small proportion of fat and of inorganic or mineral salts.

The blood corpuscles are of two kinds, namely, the red corpuscles and the white corpuscles.

The red corpuscles are much more numerous than the white (about 450 times) and average in man the enormous number of 5 millions per cubic millimetre; it is to the red corpuscles that the red colour of the blood is due. When the blood is shed it rapidly sets into a jelly and clots, i.e., is transformed into a soft and moist mass; this phenomenon is termed coagulation. As the process of coagulation goes on, the jelly-like clot contracts and squeezes out of itself a straw-coloured fluid called serum, in which the shrunken clot floats. The clot consists of threads of fibrin in which the blood corpuscles are entangled. Thus the blood serum is the plasma deprived of its fibrin. The clotting of the blood may be prevented by artificial means, such as the addition of salt or by beating it with a small brush or broom when the fibrin will settle on the hairs of the brush.

The red corpuscles can only be seen with the microscope; in a freshly drawn film of blood, they arrange themselves in rouleaux like piles of coins. Each consists of a delicate colourless elastic envelope with a coloured fluid content, which is mainly a solution of a red substance termed hemoglobin, a complex nitrogenous compound containing iron. This hemoglobin is of the highest importance, as it forms a loose combination with oxygen, and acts as the oxygen carrier of the blood. It always contains a certain proportion of this gas, but when saturated with it, it becomes of a

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brighter red colour and is then called oxyhemoglobin, whereas, when deprived of it, i.e., when it assumes the state of reduced hemoglobin, it is of a darker red. This explains the difference in the colour of the arterial blood which is saturated with oxygen, while the venous blood is much darker, since its hemoglobin has lost the greater part of the oxygen it originally contained.

The white blood corpuscles, often called leucocytes (to which we have alluded in page 15) are of irregular shape. Like the amœba, they are capable of spontaneous movement, of reacting to external stimuli and also of reproducing by division. They are true cells, exhibiting the rare instance of a living cell retaining its individuality in the body of a higher being. As we have seen before, they act as living creatures, creeping from place to place by putting out and drawing in processes (pseudopodes), and taking into their own protoplasm particles of matter which they encounter on their way. At times, they pass out through the thin walls of the capillary vessels into the surrounding tissues, especially when an injurious foreign body intrudes in those tissues. Broadly speaking, and as we shall see more fully in studying the process termed inflammation, the white corpuscles are the scavengers of the body, and their function is to engulf and to remove all harmful bodies.

The blood supplies nutriment to the cells and tissues of every organ of the body, obtaining this nutritive matter from the food digested in the alimentary canal. It further carries away from all parts waste material which is afterwards removed from it by the excretory organs. Another function of the blood, performed by the red corpuscles, is to carry oxygen to the tissues which take it up and unite it with some other element or compound resulting in the formation of substances of no further use to the body, and which are termed waste products. The most abundant of these waste products is carbonic acid gas. The living tissues take oxygen from the blood and return it later on as carbonic acid gas.

The blood, during life, is in constant motion, leaving the heart by the arteries and returning to it by the veins via the capillary vessels.

We cannot go into details in the subject of the working of the heart, and we refer the reader to one of the text-books of physiology mentioned previously. For our present purpose we shall merely describe the heart and the circulatory organs generally, insomuch as the subject is concerned with our work.

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**The Heart and the Circulation of the Blood.**

The heart consists of four chambers, two on either side, the right and left auricles or upper chambers and the right and left ventricles or lower chambers. One auricle or one ventricle does not communicate with the corresponding one on the other side, but each auricle is in communication with the corresponding ventricle by a valve which opens from above downwards, i.e., allows the flow of blood to pass from an auricle into the ventricle on the same side but does not permit a flow in the opposite direction. The venous blood, i.e., the blood which has performed its purpose of nutrition in various parts of the body, flows into the right auricle through the superior and the inferior vena cava. Thence it passes into the right ventricle through the communication valve and the contraction of the walls of the right ventricle pumps the blood into the lungs via the pulmonary artery.

In the lungs, the venous blood gives up its carbonic acid gas as well as some water in the form of steam, and takes from the air a corresponding amount of oxygen. As already pointed out, in the lungs, like in any other organ of excretion, the blood and the air breathed in are only separated by an exceedingly thin porous membrane through which the double flow of gases can readily pass. In this way the oxygenated or arterial blood flows back via the pulmonary vein to the left auricle, passes into the left ventricle through the communication valve and from the left ventricle it is pumped in the state of arterial blood, first through a main artery called the aorta and thence to all the arteries in the body.

As the aorta receives all the arterial blood issuing from the left ventricle it is, of course, the largest artery in the body, but as it divides into branches these become smaller in size and by successive division give rise to smaller and smaller arteries, which are distributed to practically every part of the body except a few which have been enumerated in page 3.

The larger arteries have very thick walls, which are made of three layers: (1) a thin internal lining of endothelial cells united at their edges by a little cementing substance; (2) a middle muscular coat; (3) a tough outer coat of connective tissue. The middle coat consists of plain, or unstriped fibres, and of elastic fibres. The outer coat also contains elastic fibres, intermixed with the connective tissue fibres.

The lumen or bore, i.e., the internal diameter of arteries, varies from about 3 mms. in the aorta to a little more than $\frac{1}{2}$ mm. in the smaller arteries.

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The smallest arteries gradually lose their outer and middle coat, and later become so small that their internal diameter is only about 1-100th of a millimetre, there being left only the inner layer of epithelial cells to form their exceedingly thin walls. These vessels are called capillary vessels and it is whilst passing through them that the arterial blood gives up to the surrounding tissues its nutriment (derived from digestion) and its oxygen (derived from respiration). It receives, at the same time, the carbonic acid gas and the other waste products and thus becomes venous blood again.

There is only a thin membrane separating the blood in the capillaries from the surrounding tissues and fluids, and this readily permits of diffusion, the nutritive material in solution or in suspension in the blood as well as the oxygen carried by the hemoglobin of the red corpuscles passing from the capillaries into the surrounding tissues while the waste products pass into the blood from the same tissues.

The capillary vessels increase in size owing to the fact that many join together and hence the volume of blood carried becomes greater. The thin walls of the capillaries become strengthened by additional coats, and the vessels become veins. These unite to form larger ones, which in their turn unite again, until near the heart there are only two large venous trunks called the venæ cavæ conducting the venous blood into the right auricle. Thence the venous blood passes into the right ventricle, from which it is pumped via the pulmonary artery into the lungs, in which it gives up its carbonic acid gas and takes up oxygen, thus returning to the left auricle in the form of arterial blood. From the left auricle it passes into the left ventricle, which again pumps it once more through the whole body.

Exactly as each auricle communicates with the corresponding ventricle by a valve which allows a flow of blood from the auricle into the ventricle but not in the opposite direction, in the same way the openings into the heart of the pulmonary artery (in the right ventricle) and of the aorta (in the left ventricle) are guarded by valves which allow of the flow of the blood in one direction only, i.e., from the heart and not into it. Diseases or malformations of these valves cause a regurgitation of blood in the wrong direction and constitute what is termed in medical work a valvular disease.

We have pointed out before that the aorta and the larger arteries which arise from successive branching of this main arterial trunk contain so much elastic tissue in their walls that they act really as elastic tubes, this elasticity playing a most important part in the work of circulation of the blood.

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The walls of the four chambers of the heart are of muscular nature, and are thicker and therefore more powerful in the case of the ventricles, especially the left one, than in the case of the auricles. The sudden contraction of the walls of the left ventricle is sufficient to cause the arterial blood it contains to flow into the aorta and thence into the various arteries, but if those vessels were merely rigid tubes, the effect of contraction of the left ventricle would not be sufficient to propel the blood as far as the capillary vessels. The elasticity of the arterial walls plays an important part in this propelling. When a mass of blood enters the first portion of the aorta, the vessel dilates in that portion owing to its elasticity, then it relaxes, and thus squeezes the blood into the next portion, since a flow back to the heart is prevented by the valve fitted at the entrance of the aorta in the left ventricle. A similar effect occurs in the pulmonary artery, which proceeds from the right ventricle. In elderly subjects, or in those cases in which the arterial walls lose their elasticity and become more or less rigid tubes, the circulation of the blood is considerably hampered; the condition is termed *arterio-sclerosis*, which means hardening with a corresponding loss of elasticity in the arterial system.

**Blood Pressure.**

During normal life the arteries are always so full of blood that their walls are in a state of tension, which gives rise to what is called the blood pressure. This is shown by the spurting out of blood when a large artery is cut. The blood pressure can also be ascertained by placing a vertical tube in an artery when, in the case of a large artery near the heart, the blood will be forced up about 5 feet, or 1.5 metres.

Just as the blood is pressing against the internal wall of the larger arteries, the latter, owing to the elastic fibres they contain, press with equal force upon the contained blood, thus squeezing it onwards towards the capillaries since it is prevented from going back into the heart by the closure of the valve. At each contraction of the left ventricle more blood is forced into the already distended aorta and the arteries branching from it, stretching these vessels still more, and this extra expansion travelling along the arterial system constitutes what is known as the arterial pulse or simply the pulse.

The pulse wave travels at the rate of about 9 metres (or 30 feet) per second, but does not as a rule extend to the capillaries and to the veins, being extinguished by the friction the blood has to overcome, especially from the greater sectional area of the capillaries. In the capillary

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vessels, and in the veins which derive from the capillaries, the jerky arterial pulse is converted into a steady and continuous flow.

The fact is shown by cutting a vein, even a large one; the blood does not spurt out in an intermittent way as is the case in a section of an artery, but flows in a continuous way.

The left ventricle of the heart in a state of health contracts about 72 times per minute, as is evidenced by the pulse rate, and during each contraction of the left ventricle the arterial pressure is necessarily raised. The blood pressure is greatest in the large arteries, diminishes as the calibre of the arteries diminishes, is still less in the capillaries, and least of all in the veins. A flow back of the blood in the veins is prevented by a peculiar arrangement of valves all along the vessels, these valves being in the form of pouches or pockets which allow the blood to travel through the larger veins to the right auricle of the heart, but do not permit a return of venous blood towards the capillary vessels.

To sum up, the blood circulates in a system of tubes, the smallest (the capillary vessels) being so numerous as to form a close network in almost all tissues of the body. These capillary vessels have exceedingly thin walls composed of only a single layer of flattened cells, united at their edges. Through their thin walls oxygen and part of the blood plasma pass by diffusion into the surrounding tissues, thus providing these tissues with the nutriment they require. The nutritive fluid thus oozing out of the capillaries and bathing the living tissues is called lymph. It is important to understand that there is no actual contact between the blood and the tissues, but that the thin membrane forming the walls of the capillary and separating the two allows of the diffusion of the lymph which acts the part of middleman between the blood and the tissues. The various anatomical elements of the tissues are thus bathed in lymph from which they take up nutriment while they excrete into it their waste products.

**Lymph and Lymphatic Vessels.**

From the brief account of the work of the circulatory apparatus we have given, it follows that lymph plays a great and important part in the process constituting the nutrition of the body generally.

Lymph is a colourless fluid chiefly made of water and containing in solution, like the blood plasma, proteids, carbohydrates and mineral salts, though the proteids are somewhat less and the water more in proportion than is the case in the blood plasma. Lymph also contains some white

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corpuscles which have passed out of the capillary blood vessels, but few or no red corpuscles. As well as the oxygen and nutritive material passing from the capillary vessels to the lymph in the surrounding tissues there is also a passage in the opposite direction of carbonic acid gas and other waste products from the tissues to the lymph, and thence into the capillary vessels and onwards into the veins and ultimately into the lungs via the right auricle and the right ventricle of the heart.

A certain amount of the lymph bathing the living tissues does not find its way directly into the capillary vessels, but returns to the blood stream in a roundabout way.

The excess of lymph from the blood (together with the white blood corpuscles it contains) which does not pass directly into the capillary vessels, lies in minute spaces (or lymphatic spaces) between the cells or fibres of the tissues, especially the connective areolar tissue. These spaces constitute the origin or beginning of very minute tubes (lymphatic vessels) which gradually unite to form larger and larger vessels through which the lymph is ultimately emptied into the venous stream a short distance from the latter's entrance into the right auricle of the heart.

Like the veins, lymphatic vessels have valves in their interior, the free edges of which point towards the heart, and the pressure caused by muscular movements thus drives the lymph onwards in the direction of the heart, the valves preventing any flow in the opposite direction.

The lymphatic vessels of the small intestine are called *lacteal* because, beside imbibing the ordinary tissue lymph, they also absorb from the intestine the emulsified fat of the food and then, after a meal, become filled with a white milky fluid termed *chyle*. The carbohydrates and the proteids of the food, on the other hand, pass from the intestine directly into the blood stream through the walls of the capillary vessels.

All the lymphatic vessels from the lower limbs, the lower parts of the trunk, the intestines and the left side of the body finally unite into a single trunk (the thoracic duct) which empties into the large veins at the root of the neck on the left side. The lymphatic vessels from the right side of the body, and from the right upper limbs similarly open into the veins on the right side of the neck.

All lymphatic vessels, including the lacteal vessels from the intestine, pass on their way to the thoracic duct through small structures termed lymphatic glands, which are really factories for the production of white blood corpuscles. As the lymph percolates through the glands it carries away with

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it many of these new white corpuscles. Lymphatic glands also act as filters, the white blood corpuscles present seizing and destroying any foreign bodies in the lymph such as bacteria, as we shall see presently in investigating the process of inflammation.

**Animal Heat and its Regulation.**

It has been repeatedly stated that heat is being constantly given off from the skin and the air passages, and anything that passes out of the body carries away with it a certain quantity of heat. Now, it is obvious that the surface of the body is much more exposed to cold than its interior. Yet the temperature of the body in health is very evenly maintained at all parts and, within the range of less than two degrees, it averages 37° C. (or 98.6° F.).

This is the result of three conditions: (1) Heat is constantly being generated in the body, as we have seen before; (2) it is constantly being distributed through the body; and (3) it is subject to incessant adjustment as regards both loss and production.

Heat is generated whenever oxidation takes place. All the tissues of the body are constantly undergoing oxidation, the living substance of these tissues built up out of the complex proteids, carbohydrates and fat contained in the food are, by means of the oxygen brought by the arterial blood, broken down into simpler and more oxidised bodies which are ultimately reduced to urea, carbonic acid gas, and water. Whenever life is being manifested these oxidative changes are going on more energetically in some places, in some tissues or in some organs, than in others. Hence, every capillary vessel and every island of extra-vascular tissue is really a small fireplace in which heat is evolved in proportion to the activity of the chemical changes which are going on.

The chief seat of this heat production is undoubtedly in the muscles, which form about half the body weight, and are carrying on an active oxidation even when at rest; this gives rise to heat, and when a muscle enters into activity or contraction, the heat production is so increased as to produce an actual rise of its temperature. After the muscles, the liver may be regarded as the next great heat producing organ.

The vital activities of the different parts and organs are very different at different times, and some parts are so situated as to lose their heat, by conduction or by radiation, more easily than others. It follows that the temperature of the body would be very different in different parts, and at

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different times if it were not for the arrangement by which the heat is distributed and regulated.

Whatever oxidation occurs in any part raises the temperature of the blood which is in that part at the time, to a proportional extent. But this blood is swiftly hurried away into other regions of the body, and rapidly gives up its excess heat to them. On the other hand, the blood which, by being carried to the vessels in the skin on the surface of the body begins to have its temperature lowered by evaporation, radiation, and conduction, is hurried away, before it has time to get thoroughly cooled, into the deeper organs, and in them it becomes warm by contact, as well as by the oxidating processes there going on. Thus, the blood-vessels and their contents may be compared to a system of hot-water pipes, through which the warm water is kept constantly circulating by a pump, while it is heated not by a great central boiler, as usual, but by a multitude of minute gas jets, disposed beneath the pipes, not evenly, but more here and fewer there. It is obvious that, however much greater might be the heat applied to one part of the system of pipes than to another, the general temperature of the water would be even throughout if it were kept moving with sufficient quickness by the pump. In this way, then, the temperature of the body is kept uniform in its several parts. If a system such as we have just imagined were entirely composed of closed pipes, the temperature of the water might be raised to any extent by the gas jets. On the other hand, it might be kept down to any required degree by causing a larger, or smaller, portion of the pipes to be wetted with water, which should be able to evaporate freely, as, for example, by wrapping them in wet cloths, and the greater the quantity of water thus evaporated, the lower would be the temperature of the whole apparatus.

Now, the regulation of the temperature of the human body is chiefly effected on this principle. The vessels are closed pipes, but a great number of them are enclosed in the skin and in the mucous membrane of the air passages, which are, in a physical sense, wet cloths freely exposed to the air. It is the evaporation from these which exercises a more important influence than any other condition upon the regulation of the temperature of the blood, and consequently, of the body.

But, as a further nicety of adjustment, the wetness of the regulator is itself determined, through the aid of the nervous system, by the temperature of the body. The sweat glands, as we have seen, may be made to secrete by impulses reaching them along certain nerves coming from a centre



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in the central nervous system. This centre is itself connected by other nerves with the skin, and the ends of these cutaneous nerves are so constituted that they are stimulated by heat applied to the skin. When the body is exposed to a high temperature (and the same occurs when a part only of the body is heated), these cutaneous nerves convey impulses to the central nervous system, from which other impulses are then sent out along the secretory nerves to the sweat glands and cause them to pour forth a copious secretion on to the skin, and when the temperature falls, the glands cease to act. Moreover, in this work of secreting sweat, the sweat glands are assisted by corresponding changes in the blood-vessels of the skin. It has been stated that the small arteries of the body may be sometimes narrowed or constricted, and sometimes widened or dilated. Now, the condition of the small arteries, whether they are constricted or dilated, depends, as we have also seen, upon the action of certain nerves (vaso-motor nerves). It appears that when the body is exposed to a high temperature these nerves are so affected as to lead to a dilatation of the small arteries of the skin; but when these are dilated the capillaries and small veins in which they end become much distended with blood, and from these filled and swollen capillaries much more nutritive matter passes through the capillary walls to the sweat glands, so that these have more abundant material from which to manufacture sweat. On the other hand, when the body is lowered in temperature the vaso-motor nerves are so affected that the small arteries of the skin are constricted; hence less blood enters the capillaries of the skin and less material is brought to the sweat glands.

Thus, when the temperature is raised two things happen, both brought about by the nervous system. In the first place, the arteries of the skin are widened so that a much larger proportion of the total blood of the body is carried to the surface of the skin and there becomes cooled; and secondly, this cooling process is greatly helped by the increased evaporation resulting from the increased action of the sweat glands, whose activity is further favoured by the presence in the skin of so much blood. Conversely, when the temperature is lowered, less of the blood is brought to the skin, and more of the blood circulates through the deeper hotter parts of the body, and the sweat glands cease their work (this quiescence being in turn favoured by the lessened blood supply); hence the evaporation is largely diminished, and thus the blood is much less cooled. Hence it is that, so long as the surface of the body perspires freely, and the air passages are abundantly moist, a man may

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remain with impunity, for a considerable time, in an oven in which meat is being cooked. The heat of the air is expended in converting this superabundant perspiration into vapour, and the temperature of the man's blood is hardly raised.

The temperature of the body is kept constant by that carefully adjusted variation in loss of heat from its surface which has been described in the preceding section. But now we may point out that there is another way by which this constancy might be attained, namely, by altering the production of heat taking place in the body, in correspondence to the changes in the surrounding temperature; just as the temperature of a room may be regulated by putting out or increasing the fire as well as by opening or closing its windows. The question thus raised is very interesting, but it is also very abstruse, and we must not do more than just touch upon it.

All oxidation in the body involves the consumption of oxygen, the production of carbonic acid and the generation of an exactly corresponding quantity of heat. We may, therefore, take the difference in the amount of oxygen used up (and of carbonic acid produced) at different times as a measure of the amount of heat being produced in the body during the same periods. Working in this way it is found that when a warm-blooded animal is exposed to cold, as when it is put into a chamber which is cooled, it uses up more oxygen and gives off more carbonic acid than when put into a warm chamber. But this can only mean that in the cooler surroundings the animal produces more heat than when the surroundings are warm. Again, we may point out, as tending to the same conclusions, that our desire for food is greater, on the whole, in the cooler winter time than in the warmer summer, since all food is oxidised in the body and during this oxidation gives rise to heat. Thus there are reasons for supposing that within certain limits altered production of heat may play some part in keeping the temperature of the body constant.

All the functions of the body which we have so far studied have been seen to be under the guidance of nervous impulses. We may, therefore, suppose that the production of heat is no exception to the rule, and, indeed, there are reasons, based largely on experiment and partly on the phenomena of certain diseases, which justify this view. More than this we must not say.

The condition to which the name of fever is given is characterised essentially by the temperature of the body being higher than is usual in health. Thus it may rise to as much as 41° C. (105.8° F.) or occasionally even above this

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point, and there has been much dispute as to how this high temperature arises. By many it is regarded simply as the outcome of a disturbance of the mechanism by which heat is lost to the body, some diminution in loss of heat leading naturally to a rise of temperature, and probably this is the most common cause of the rise of temperature. But on the other hand, direct measurement shows that a fevered person often gives off more heat than usual, and at the same time uses up more oxygen and produces more carbonic acid and urea than is usual. In such cases there is no doubt that the abnormally high temperature is largely due to an over-production of heat.

**The Ductless Glands.**

There are not a few processes occurring in the living body which are so hidden as not to be at all evident to a superficial examination, yet these processes are of the utmost importance. In recent years a remarkable discovery has been made with regard to certain organs which had up to then been a puzzle to physiologists and were mainly regarded as remains of active organs rendered unnecessary by the process of evolution and adaptation of the organism to the surrounding conditions. Such organs are: (a) the suprarenal bodies which are found immediately above the upper end of each kidney; (b) the thyroid body or thyroid gland, a mass weighing about 30 grammes and located under the thyroid cartilage or the larynx (or Adam's apple) and assuming the form of a crescent embracing the larynx and the upper part of the windpipe; (c) the thymus gland, which is in the neighbourhood of the thyroid body, in front of the windpipe; (d) the pituitary gland in the lower part of the brain; (e) the spleen, lying on the left side of the stomach; and (f) various organs now known to belong to the lymphatic system such as the lymphatic glands, the tonsils and the glands of Peyer found in the walls of the lower portion of the small intestine.

All these organs agree anatomically in having the usual structure of glands, but whereas ordinary glands have one or several ducts or canals through which their secretion is poured out, the above ones have no duct, and for this reason are often termed ductless glands; they are only connected with the rest of the organism by their blood-vessels. That they play an important part in the physiological work of the body is clearly shown by the accidents following their removal. The products elaborated by these ductless glands are called internal secretions. We are going now to study briefly some of the most important features of the ductless glands and their internal secretions.

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(a) The suprarenal capsules were at one time thought to have something to do with the formation or modification of pigment, and this is probably true, since in the curious disease called Addison's disease which is characterised by an excessive bluish black pigmentation of the skin, as well as with various nervous troubles, there is always an insufficiency of the capsular internal secretions.

An animal in which the suprarenal capsules are removed always dies, but before this happens various nervous troubles are observed, the muscles become weaker, assume a flabby appearance, and finally are paralysed altogether. The symptoms thus created by the removal of the suprarenal capsules are similar to those due to poisoning by curare, the substance used by Indians to coat the ends of their arrows and spears.

The purpose of the capsules seems therefore to be the secretion of an antitoxin which neutralises the toxin or poison produced in a muscle when at work.

A crystallisable substance of complex chemical composition, called adrenalin, has been discovered in the secretion of the capsules, and can now be produced synthetically in the laboratory.

Adrenalin has the effect of stimulating non-striated or smooth muscular fibres and therefore of constricting most energetically the calibre of the small arteries, the coats of which are supplied with smooth muscular fibres. As the heart beats are not affected, it follows that after an injection of a minute amount of adrenalin the pressure of the blood in the larger arteries will be much increased, a condition favourable, within certain limits, to a vigorous circulation.

Since every 1,000 grammes of normal blood contains about the thousandth of a milligramme of adrenalin, and since this proportion increases when the blood pressure tends to diminish owing, for instance, to fright or to some other emotion, it is logical to conclude that the adrenalin of the normal blood, secreted by the suprarenal capsules, intervenes to keep the blood pressure at its normal level.

Owing to its constricting effect on fine arteries, adrenalin is used medically as a powerful styptic (i.e., astringent) by which bleeding may be arrested.

Beside the above property, adrenalin acts as a stimulant of the sympathetic nervous system. In any case in which the moderating power of the vagus or pneumogastric nerve (10th nerve) is increased, there is a hypersecretion of the suprarenal capsules, i.e., an increase of adrenalin in the blood, which acts on the sympathetic ganglia to counterbalance the moderating or inhibiting effect of the vagus.

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(b) The thyroid body or thyroid gland also plays an important part in the general nutrition of the body. Its excessive development constitutes the condition known as goitre.

The removal of the thyroid gland in dogs causes partial paralysis, then convulsions, during which the temperature of the body is raised and the secretion of urine very reduced. The animal soon dies though young ones may survive, but then their bodily development is considerably slowed down. After eight months, a young dog or a young sheep submitted to the operation only reaches about half the size of the normal animal of the same age, and presents all the symptoms of the condition known in the human being as cretinism or imbecility.

It is a fact known for a long time that the removal of a goitre in the human being has very far-reaching effects; if the operation is performed in children the growth of the body and the development of the intellectual faculties are arrested, the subject becoming affected with cretinism. In adults, the face becomes puffy, and assumes a vacant appearance, the hands increase in size, the hair falls off, and the cerebral faculties diminish to such an extent that in a few years the subject becomes an imbecile. In some cases he dies from tetanic convulsions. These examples show that there is undoubtedly a connection between the atrophy or the removal of the thyroid gland and the growth of the body as well as the development of the intellectual faculties; the exact relationship is not known at present, but it is probable that in the absence of the thyroid gland, the organism is poisoned by toxins generated in the cellular elements of the body. This is proved by the fact that the urine of a dog whose thyroid gland has been removed is much more toxic than that of a normal animal; the purpose of the thyroid gland is no doubt the secretion of an antitoxin which neutralises the toxins as they are being formed. It has been found that the thyroid body secretes a chemical substance termed thyroidin which contains iodine, and which has the property of destroying the mucinoid material which is so apparent in the face, the hands and in most parts of the body in those subjects in which a goitre, i.e., the thyroid gland, has been removed.

At all events, atrophy or removal of the thyroid gland produces the same symptoms as a curious disease called myxœdema, i.e., muscular weakening, infiltration of the cellular tissues by a mucinoid matter together with anæmia or deficiency of red blood corpuscles. As the convulsive accidents occurring after removal of the thyroid gland are

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not observed in subjects affected with myxœdema, the inference is that the thyroid gland has other functions still unknown. Myxœdema is curable by administration of raw thyroid gland or powdered thyroid gland, or again, of thyroidin extracted from the gland of the sheep or some other mammal. The same treatment has proved satisfactory to accelerate the bodily and intellectual development of backward children.

(c) The thymus is another glandular organ in the neighbourhood of the thyroid, in front of the windpipe and behind the breastbone or sternum. It is formed of two distinct lobes, each of which is made of small glandular masses joined together. It constitutes what is called sweatbread in young ruminating animals. It is highly developed in children and gradually diminishes in size in the adult, sometimes disappearing altogether and being replaced by a mass of ordinary fatty tissue. Its functions are not well elucidated. As a rule, those animals in which it is removed have their normal development and growth considerably slowed down, but after a time the regular growth resumes its ordinary course.

Extract of thymus gland absorbed in the system, either through the mouth or by hypodermic injections, causes a lowering of the blood pressure and an acceleration of the heart beats.

(d) The pituitary body or pituitary gland has been already mentioned (page 63). It seems to exert an influence on the growth and development of bone. In all cases in which it has been possible to remove it serious troubles of general nutrition similar to those resulting from the removal of the thyroid gland have been observed, hence the conclusion that the functions of these two ductless glands are probably similar. A morbid condition of the pituitary gland gives rise to the curious disease termed acromegaly, in which, beside nervous symptoms and a peculiar kind of ocular trouble, to which we shall refer later on, there is an enormous development of the bones of the face, the hands and the feet.

(e) The spleen is the largest of the ductless glands; it weighs about 200 grammes, is red in colour, of oval shape, and located in the abdomen on the left of the stomach. It has no communication with the digestive apparatus, and is attached to the stomach and to the diaphragm by folds of the peritoneum (the serous membrane in the form of a closed sac the two laminæ of which surround, invest and connect all the viscera of the abdominal cavity).

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The spleen is externally covered by a strong fibrous capsule, and passing from this capsule in all directions into the interior of the organ are partitions or septa of connective tissue and unstriated muscular tissue dividing the gland into numerous compartments. These are filled with spleen pulp consisting of a network of fine fibres in the meshes of which are numerous granular or pigmentary corpuscles and red blood corpuscles.

The spleen receives a considerable quantity of arterial blood out of all proportion with its size; the splenic artery has an internal diameter of 1 c.m. at the point it enters the gland; this artery breaks up into branches like the twigs of a tree; there are no capillaries in the spleen, the arterial blood merely permeating the pulp; from the spaces in which the pulp lies, veins originate which by confluence ultimately form the splenic vein which carries the blood that has passed through the spleen into the liver and thence into the general venous stream.

The physiologic purpose of the spleen has long been unknown, and various philosophers attributed to this gland a psychologic function, but differed in the nature of the function itself; thus in English, the term spleen is associated with a melancholic and depressed outlook, while there is a French idiom, "se dilater la rate" (or to dilate one's spleen) which is equivalent to uproarious laughter.

It is ascertained now that in the young the spleen is the organ in which both the red and the white corpuscles of the blood are formed, while in the adult the function of the spleen is merely reduced to the destruction of effete red corpuscles.

A careful microscopic examination shows that the pulp is almost entirely composed of cells in which it is possible to recognise the differentiated elements of the blood, in other words, some of these cells are ordinary white corpuscles, while the others, of a reddish tint, may be regarded as young red corpuscles in process of formation at the expense of the white corpuscles. The development of the spleen has been carefully studied in lower animals. At the outset the gland is simply a mass of colourless cells of mesodermic origin enclosed in a network of connective fibres in which the blood finds its way. The cells gradually separate from the mass to which they originally belonged, become loaded with hemoglobin and thus are transformed into real red blood corpuscles, which fall in the blood stream; others remain in the state of white blood corpuscles.

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Though a similar observation has not been made in mammals, yet two facts are proofs that the same mechanism is at work: (1) if one stimulates the nerves distributed in the spleen the blood which issues from the gland is much richer in red corpuscles than it is in ordinary conditions; (2) the extirpation of the spleen in a dog causes a diminution in the number of red corpuscles in the blood. Moreover, the splenic pulp of the adult shows the presence of distorted or fragmented red corpuscles sometimes reduced to the state of mere pigmentary granules. This would support the theory that, in the adult at least, the spleen is the organ in which used up red corpuscles are destroyed while, on the other hand, the formation of these corpuscles is most intensive in the young.

The pulp contains curious masses of lymphoid tissue called Malpighian corpuscles, which are closely connected with the branching blood-vessels. These corpuscles become gradually converted into white blood corpuscles.

(f) The tonsils or amygdales are two small fleshy masses located on each side at the back of the pharynx. They are formed, like all other ductless glands, of cells embedded in a network of connective tissue. The part they play in the physiological work of the body is, however, of small importance, since they can be removed with impunity when their excessive development is an obstacle to the proper performance of the movements of deglutition or interferes with respiration. The extirpation of the tonsils in such cases has never been accompanied by troubles of nutrition or by distressing nervous symptoms.

**Chemistry of the Body.**

To conclude our brief survey of the physiological work of the human organism, we must say a few words on the chemistry of the body generally.

It is a well-known fact that matter, whether it occurs in the solid or the liquid or the gaseous form, is made either of elements, i.e., of substances which cannot be resolved into simpler substances by any chemical or physical process, or of compounds or combinations which are formed by the chemical union of two or more elements.

There are between eighty and ninety elements known to the chemist, fourteen of which enter into the composition of the human body. These are Oxygen, Hydrogen, Carbon, Nitrogen, Sulphur, Phosphorus, Chlorine, Sodium, Potassium, Calcium, Magnesium, Iron, Fluorine, and Silicon, the

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first four forming about 85 per cent. of the whole bodily frame. Other elements, such as Manganese and Lead, are occasionally found, but only in very small quantities.

Oxygen and nitrogen may occur in their free state dissolved in the blood, though they are more often found in combination with other elements in the various tissues of the body. Likewise, hydrogen is occasionally found in the intestines as the result of some putrefaction process, but in a general way the main chemical elements of the body are always united to form chemical compounds or combinations.

These compounds or proximate principles, as they are termed in physiology, are either (a) Mineral or Inorganic Compounds, or (b) Organic Compounds.

The first class includes, beside the elements themselves, acids such as hydrochloric acid and salts such as calcium carbonate or calcium sulphate. Water, i.e., a combination of oxygen and hydrogen, in the proportion of two atoms of hydrogen for one atom of oxygen, belongs to the category of inorganic compounds.

The second class includes numerous complex compounds of oxygen, hydrogen, and carbon, with or without nitrogen.

In what follows we shall briefly describe the most important amongst the inorganic and organic compounds occurring in the human body.

**Chemical Elements and Inorganic Compounds.**

Oxygen (O) is an invisible gas, forming about one-fifth of the total volume of the atmosphere. It presides to combustion, and is absolutely necessary for animal life. It occurs in its free state in the air passages of the lungs, whereas in the blood it forms a loose and unstable combination with the hemoglobin of the red corpuscles; these corpuscles act as the carrier of oxygen to all parts of the body in which this element is liberated so as to serve to the oxidation or combustion of the tissues, as we have seen before.

Nitrogen (N) is an invisible gas forming about four-fifths of the total volume of the atmosphere. We say "about" since fresh pure country air contains in every 100 parts in volume, 20 parts of oxygen, 79 of nitrogen, together with a small fraction, 0.04, of carbonic acid gas, and a variable quantity of water in the form of steam. The researches of Lord Rayleigh have shown that the air also contains a small proportion of another gaseous element he called Argon (which means the lazy one), an inert substance

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which is reckoned here with nitrogen. The fact that argon had escaped observation of chemists until Lord Rayleigh discovered it is explained by its lack of any tendency to combine with other elements.

Nitrogen occurs free in the air passages, and is dissolved to a very slight extent in the blood. In combination with other elements, it forms the greater part of the substance of the body, many of its compounds being of the utmost importance, as we shall see presently.

Hydrogen (H) is a light, invisible and combustible gas. A little free hydrogen is occasionally found in the intestines arising from the fermentation of certain food products, but it mainly occurs in combination with other elements, and is present in many of the constituent parts of the body.

Carbon (C) is a solid element existing in a variety of forms; for instance, blacklead or graphite and diamond are natural conditions of carbon, while charcoal is an artificial form. When carbon burns, it unites with the oxygen of the air and forms carbonic acid gas or carbon dioxide ($CO_2$). Carbon exists in a number of combined compounds in almost all tissues of animal and vegetal beings, but it does not occur in the body in its free state. The oxidation or burning of carbon compounds in the tissues of the body liberates a certain amount of heat, as we have pointed out before, and results in the formation of carbon dioxide as one of the most important waste products of life.

The other elements of the body, beside the four we have just mentioned, are only found in small amounts and not in their free state, but in combination with other elements.

It should be remembered that air is a mixture of oxygen and nitrogen, with a small proportion of carbonic acid gas and of argon.

The inorganic compounds of the body are water; acids, such as hydrochloric acid, a combination of hydrogen and chlorine which exists in small quantity in the gastric juice, and plays an important part in digestion; salts, as calcium carbonate and calcium phosphate which form the mineral part of bone, sodium chloride or common salt, a combination of sodium and chlorine which is found in the blood serum and in many other liquids of the body.

Water, a combination of oxygen and hydrogen, is found in greater or smaller proportion in all the living tissues, and forms about two-thirds of the weight of the whole body.

Many inorganic salts, beside those stated just now, exist in the body, but only in small quantities. When a body is cremated, various compound gases, chiefly carbon dioxide,

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ammonia and watery vapours are formed, and escape into the atmosphere, whilst the ashes which remain are mainly composed of the incombustible inorganic salts.

**Organic Compounds.**

Every separate living organism, animal or vegetal, is formed of various substances or tissues made of cells and fibres (which are merely elongated cells). These anatomical elements, which may be regarded as having an independent life, build up living matter out of the food supplied to them. In the case of plants, this food consists mainly of the simple inorganic substances found in the soil, and of the carbon dioxide of the atmosphere from which the carbon entering into the composition of the cells is obtained. In other words, plants live on simple inorganic materials derived from the soil and the air, and convert them into those complex organic substances which form their tissues.

On the other hand, man and other animals cannot convert inorganic materials, except water, into the living substance of the body, and therefore they must feed on the organic substances formed by plants or supplied by the tissues of other animals that have lived on plants.

The organic compounds of the body belong to three great groups, namely, proteids, or albuminous bodies, carbohydrates and fats.

The proteids are complex nitrogenous bodies containing carbon, hydrogen, oxygen and nitrogen, with a small variable amount of sulphur.

The varieties of proteids are many, but they have a point in common, namely, that they contain nitrogen, and are the only class of food products which contain this element. Living tissues require nitrogen for growth and reparation processes and, for this reason, proteids are often called tissue builders. They can also be used as fuel, being oxidised to produce water, carbonic acid gas and urea, though the chief fuel or heat-producing ingredients of food are carbohydrates and fats.

Proteids occur in a semi-solid, viscous condition, or in solution, in nearly all the solid and liquid parts of the body. They are most abundant in the lean meat of all animals, the white of eggs, and in some vegetables like peas and beans. With the exception of the hemoglobin of the red blood corpuscles (which is really a compound of a special form of proteid called globin, with hematin) they are all amorphous or non-crystallisable. They are insoluble in alcohol and ether. Some are soluble in water, others are insoluble, but most of them are soluble in weak solutions

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of neutral salts (like sodium chloride or common salt and magnesium sulphate); a few of them are only soluble in concentrated saline solutions.

Proteids are never absent from the protoplasm of active living cells, whether animal or vegetal, and they are intimately connected with every manifestation of organic activity.

As we have stated before, in plants the proteids are built out of the simpler chemical compounds of the soil and the atmosphere. In animals, such a direct synthesis never occurs, the proteids being derived directly or indirectly from plants. By the action of certain digestive juices, all proteids are capable of being converted into closely allied substances called peptones which, after absorption, undergo a reconversion into proteids.

An important property of proteids is that they are non-diffusible, i.e., they belong to the category of substances which cannot pass through an animal membrane and are for this reason called colloid substances by contradistinction with crystallisable solutions which are readily diffusible. Peptones are, however, diffusible. The term albuminoid is restricted to denote certain nitrogenous substances closely allied to proteids though differing from them in some respects. We have stated before that all connective tissues yield gelatine on being boiled in water. The gelatine thus obtained sets in a jelly when the solution in hot water is allowed to cool. Gelatine is an instance of an albuminoid substance. Other instances are mucin and chondrin. Mucin is the albuminoid that forms the secretion of certain epithelial cells; it is the chief constituent of mucus and gives its sliminess to the secretion of mucous membranes. Chondrin is the albuminoid formed from cartilage on boiling it with water, and is probably a mixture of mucin and gelatine. Another variety of albuminoid is keratine, the highly insoluble substance which replaces the protoplasm in the surface cells of the epidermis, in nails and in hair.

Though gelatine is easily digested, being converted into a peptone-like body which is readily absorbed, yet it will not entirely replace proteids, but only acts as a proteid-sparing food. The part played by gelatine in nutrition is of importance since jellies are so often given to invalids. Voit, who has studied the subject carefully, has found that gelatine does not entirely replace proteids, and that animals fed on it alone rapidly waste away. In conjunction with a small amount of true proteid, gelatine is, however, capable of maintaining nitrogenous equilibrium as well as if only nitrogenous food of proteid nature were taken.

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Carbohydrates are compounds of carbon, hydrogen and oxygen, there being always two atoms of hydrogen for every atom of oxygen, i.e., the same relative proportion as in water. They are chiefly derived from vegetal tissues, and form an important class of food products. The substances known as starches and sugars belong to this class. They are oxidised or burnt in the tissues of the body and become converted into carbon dioxide and water vapours, such changes being accompanied by a generation of heat.

Fats are also organic compounds containing carbon, oxygen, and hydrogen, but the proportion of oxygen is smaller than it is in carbohydrates. Fats and oils are found in the tissues of some animals, in milk and in certain seeds. The oxidation of fat is one of the chief sources of heat to the body, a given amount of fat producing more heat energy than the same weight of any other foodstuff.

**Ferments or Enzymes.**

Certain minute organisms possess the power of inducing definite chemical changes in the fluids, or other media, in which they live. One of the most interesting chapters in the history of scientific discovery has been that of the nature of fermentation. Fermentation and putrefaction have been known from early times, but their true nature has been discovered only in comparatively recent years. It is known now that both are connected with the life history of micro-organisms or bacteria. For instance, in the ordinary fermentation of sugar and its transformation into alcohol, carbonic acid gas and other substances, the main agency is that of various kinds of yeast cells. The putrefaction of dead nitrogenous matter is likewise due to the activity of various bacteria. Other micro-organisms can lead to the formation of vinegar or acetic acid from alcohol, to the souring of milk by the production of lactic acid, etc. These living organisms are spoken of as organised ferments. In another class of chemical changes, the result is due not directly to living organisms but to chemical substances derived from or elaborated by living cells, these substances having the property of inducing chemical transformations in a large mass of certain other substances without themselves undergoing noticeable alterations. These substances, or these agents, are spoken of as unorganised ferments or soluble ferments or enzymes.

A recognition of these facts and of the part played by bacteria in many diseases has led to the evolution of the vast realm of knowledge now known as bacteriology.

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Physiologists have long been acquainted with the existence in the body of soluble ferments like the ptyalin of the saliva, which changes starch into sugar and the pepsin of the gastric juices, but it is only recently that there has been an adequate recognition of the parts played by soluble ferments in many physiological processes. It is now known that all soluble ferments or enzymes are formed in the interior of cells. It was thought at one time that the yeast cell effected fermentation in the juice of the grape, or in a solution of sugar, by its own vital activity; this view was supported by the fact that during fermentation there is a remarkable multiplication of the cells of the yeast. It is proved now that the fermentation is due to an enzyme formed in the interior of the yeast cell and that, in a similar way, all enzymes are formed in cells, as, for instance, ptyalin in certain cells of the salivary glands, and pepsin in certain cells of the mucous membrane lining the internal surface of the stomach.

Each enzyme has a limited field of activity; this activity appears to be greatest at about 39° to 40° C.; at 50° the ferment is destroyed. Extreme cold arrests the activity of an enzyme, but does not seem to injure it, since it will again ferment if the temperature is raised to about 40° C.

A remarkable feature of the action of an enzyme is that only a small amount is necessary, and that at the end of the process this amount is the same as at the beginning. If the enzyme is used up or if a portion of it is used up, there must be a process by which the enzyme is reconstructed. It has been suggested that the enzyme acts merely by its presence, i.e., in virtue of what chemists call catalyctic force, but it is really difficult to imagine that a chemical effect can be produced in this way by the mere presence of a soluble ferment. The question is not elucidated.

As already stated, enzymes are formed in cells. Cells may be frozen and then pounded into a paste; enzymes are thus set free and, at the proper temperature, they will manifest their usual activities. There can be no doubt that as almost all living cells contain enzymes, they take part in nutritional processes by exciting changes in the protoplasm of the cell, or possibly in the substances stored in the cell. They may thus carry on metabolic changes during the life of the cell, and they may even cause destruction of the cell after death by a kind of autodigestion or autolysis.

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## CHAPTER VI.

### PATHOLOGICAL PROCESSES.

A few words on pathological processes, i.e., on what happens in certain conditions of disease, are necessary to arrive at a clear understanding of the mechanism of disease generally, and more especially, from our present point of view, of disease of the ocular organs.

It should be observed that, on the whole, pathological processes are merely modified physiological, i.e., normal, ones. Thus, serum effusion from the capillary vessels into the tissues is an ordinary process of healthy nutrition, while a similar exudation in excessive quantity causes dropsy. Likewise, the exit of the white blood corpuscles through the walls of the capillary vessels is a normal process called migration of white corpuscles or diapedesis, the purpose of which seems to be to promote the natural growth of the various tissues. If, however, the process of diapedesis is exaggerated, as is the case in the neighbourhood of an inflamed area, the white corpuscles accumulate to form new tissues, or degenerate to give rise to an abscess.

**Inflammation.**

When a foreign body is introduced into the tissues directly from outside (as is the case in a penetrating wound), or when it is brought from some other part of the body by the blood stream, certain changes take place which represent the reaction of the organism against the injurious effect of the intruding body; the purpose of these changes is to destroy or to counteract or to throw out what is noxious, and also to repair what has been injured and to restore what has been destroyed.

When an irritant body has been introduced into a tissue the blood-vessels of the affected area dilate so as to bring an excess of blood, and therefore an increased number of white blood corpuscles; these pass out of the walls of the capillary vessels into the surrounding tissues more freely than usual at the same time as a greater amount of serum. The dilatation of the blood-vessels and the passage into the tissues of an exaggerated amount of white corpuscles and serum explain the redness and the swelling observed in an inflamed area; the degree of swelling varies with the density and the vascularity of the affected part, i.e., the number of blood-vessels it normally contains. Besides redness and swelling, the other symptoms of inflammation are heat and pain, the heat

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arising from the greater cellular activity and the pain from the increased pressure on the nerves in the distended tissues.

We have stated just now that the process of inflammation is the effort of nature to get rid of the injurious effect of irritants. The white corpuscles are the cells which chiefly attack and remove foreign bodies, and for this reason they are often said to be the scavengers of the organism; their activity depends largely upon the presence of certain chemical substances in the blood plasma.

The first appreciable change in inflammation is hyperemia, i.e., dilatation of the blood-vessels, causing an excessive blood supply in the affected part, the consequence of which is redness and heat. Later on, the white blood corpuscles and the serum pass out of the capillary vessels into the surrounding tissues, which become cloudy and swollen. If the process goes on, the blood circulation, which at first was very active, slows down, the white corpuscles increasing in number and sticking to the vessel walls; at the same time, the red blood corpuscles begin to ooze through the walls of the capillary vessels, the result being the formation of a blood clot, and later on, death of the affected tissues, which become transformed into pus.

A more common termination is recovery, the blood-vessels gradually becoming less dilated and the exuded white corpuscles either passing back into the capillary vessels or breaking up into a granular material which, together with the serum, is absorbed into the general blood stream.

**Microbes or Bacteria.**

Though any foreign body introduced into the tissues may act as an irritant, and cause inflammatory reaction, yet, if that body contains no microbes, its presence is tolerated by the tissues, the latter enclosing it within a capsule; such a foreign body, if small, is gradually absorbed; if large or of a dense structure, it may remain permanently encapsuled in the tissue. The innocuousness or otherwise of a foreign body in the system does not depend so much on its size as upon the absence or presence of microbes. Microbes are very minute, microscopic living organisms consisting of a single cell, i.e., of a mass of protoplasm enclosed in an envelope and classified according to their shape and to their reaction to various staining reagents. They are very small, varying from one to a few microns. When circular in shape they are called cocci; when rod-shaped, bacilli; when more or less filamentous, spirilla.

These living organisms play a great part in the work of nature, as they break up into more or less simple



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combinations the complex molecules of the organic substances which form the bodies of animals and plants, or which are excreted by them.

Thus, the souring of milk, the ripening of cream and cheese are due to bacteria. Bacteria are also capable of secreting poisonous substances or toxins, somewhat similar to alkaloids, both within the animal body and in artificial media; each kind of bacterium produces a specific toxin, and it is this which is so inimical to the tissues of the body.

Bacteria are most sensitive to outside influences, their vitality being greatly increased or decreased by variations in temperature; some prefer warmth, some cold. Some require air, some others do not. Some grow better on such substances as potatoes, others on jellies; this artificial food is termed a culture medium. Excessive cold and, still more so, excessive heat kills them, as do certain substances called antiseptics. As a rule, antiseptics are not able to kill microbes present in the body, as the vitality of the bacteria is generally greater than that of the cells of the body; therefore the antiseptic would kill the cells without doing more than weakening the bacteria, and these would become revitalised, as they would thrive on the dead cells. This is the reason why antiseptics are of little value for the destruction of bacteria in the body, except in some very special circumstances. An aseptic substance is one which contains no living organisms, no bacteria, and in surgical operations everything is made aseptic.

Though bacteria are necessary to animal life, some of them are prejudicial, as they wage war on mankind; such is the case for the bacillus causing tuberculosis, the diplobacilli (so called because they arrange themselves in pairs, placed end to end) causing angular conjunctivitis, the pneumococci, causing certain forms of pneumonia, etc. Many forms of bacteria are present in the air, and are carried by it into all the cavities of the body communicating with the atmosphere (nose, bronchi, lungs, mouth). Others are introduced in our body by means of the food we partake of, and a number of them are of great assistance to digestion; these mostly live on dead matters which they break up into simple bodies and are termed saprophytes. There are others, however, termed parasitic bacteria, which can attack living animals and plants under certain conditions. They are found at the surface of the skin and the mucous membranes lining the cavities of the lungs, the air passages, the alimentary canal, etc., but are not present within the tissues, the epithelial cells being nature's protection against the attacks of these micro-organisms. If the epithelial cells be debilitated or injured,

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the microbes may gain entrance into the tissues. The results of such an invasion are very similar to the changes we have described under the heading of inflammation. The blood-vessels become dilated, serum and white corpuscles pass through the walls of the capillaries and the white corpuscles attack the invading organisms. If the white corpuscles are victorious, the microbes are eaten up and the affected area returns to normal again; if defeated, the cells of the tissues and the leucocytes are killed, forming, together with the toxins secreted by the microbes, a whitish yellowish fluid called pus or matter. As a rule, nature brings up more white corpuscles to resist a further encroachment of the victorious microbes, and generally a barricade of young, healthy white corpuscles surrounds the affected area and cuts it off from the surrounding parts; such a limitation of the affected area leads to the formation of a localised collection of pus called an abscess, which gradually burrows to the surface and bursts, so discharging its contents and preventing further absorption into the system of the toxins which are produced in the abscess cavity. It is to prevent this absorption of toxins and also to relieve the pain due to the pressure of the swollen tissues on the nerve-ends that an incision of the abscess is performed by the surgeon.

When the microbes overcome the barrier erected by nature, the inflammatory process extends to the surrounding parts until a considerable area is affected; the condition is termed a phlegmon.

In a general way, the ultimate result of the contest between the microbes and the resisting forces of the body depends largely on the degree of virulence of the microbes and the degree of activity of the white blood corpuscles, and the activity of the white corpuscles is, in turn, dependent upon the presence in the blood serum of certain substances called opsonins that stimulate and increase the combative power of the white corpuscles. These special substances or opsonins are distinct and specific for each kind of microbe, and it is the toxins of the latter which incite nature to produce them.

We have said that when the process of inflammation ends in recovery, the affected tissues are ultimately restored. It should be noted, however, that if an abscess or a severe inflammatory process occurs in a special tissue, for instance, a muscle, or still more so in a highly differentiated part like the retina, the affected part is not replaced by normal tissue but by ordinary fibrous tissue, and so the special function of the affected area is lost; hence the importance of cutting short the inflammatory attack in a specialised tissue.

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**Degeneration of Living Tissues.**

In a general way, when a tissue is insufficiently nourished it degenerates, i.e., it loses its highest function. Degeneration may affect any tissue in the body, but the more highly the tissue is differentiated for a special function the greater is its tendency to degenerate. This process is frequently observed in the cornea of old people in the form of an opaque whitish area (arcus senilis) concentric with the corneal margin. The transparent corneal tissue becomes transformed into an opaque or translucent tissue owing to interference with nutrition. In the same way, if the nutrition of the retina is interfered with, the normal retinal tissue with its highly complex structure is gradually transformed into simple fibrous tissue unable to react under the stimulus of light.

As stated above, when a tissue undergoes reparation after a process of inflammation, the repaired tissue is a degenerated tissue, i.e., a tissue unable to perform the function of the original tissue. It is especially so in the case of a highly differentiated tissue.

The term catarrhal inflammation is applied to denote a slight or moderate process of inflammation in mucous membranes like the conjunctiva or the membrane lining the air passages. This process causes a more congested, i.e., reddened, condition of the membrane, together with the production of an excess of mucus by the mucous glands present in great numbers in such membranes.

**Metastasis.**

It may happen that the toxins or poisons secreted by bacteria in an inflamed area are absorbed in the blood stream and are carried to another part of the system where they may cause a similar process of inflammation. The transfer in this way, through the blood-vessels, of a diseased process from a primary focus to a distant one is termed metastasis. For instance, the toxins generated by microbes which frequently lodge between the gums and the teeth may be carried to the ciliary body, in which they develop a process of inflammation or cyclitis.

**Ulceration.**

The process of ulceration is of the same nature as that of suppuration except that the discharge instead of collecting in a closed cavity and forming an abscess, at once escapes on the surface; there is thus a loss of surface epithelium which appears as an open wound or sore. An ulcer may be described as a loss of substance occurring on the skin, or a mucous membrane, or on a structure like the cornea, due to

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a gradual destruction or necrosis of the tissues. In the eye an ulcer of the cornea is not infrequent, and may be caused by a foreign body, or may be due to the attack of some microbes.

As pointed out before, if the ulceration process ends in recovery the lost tissue is repaired but, in the case of the cornea, the repaired tissue is usually degenerated inasmuch as it is not transparent like the normal tissue and the curvature of the surface of the affected area is not as regular as that of the rest of the membrane.

Tuberculosis or consumption is due to a special bacterium, a bacillus which, though commonly found in the lungs, may attack any part of the body; however, it rarely invades the eye. The resulting pus is frequently caseous in appearance (i.e., looks like cheese).

Syphilis is an infectious disease caused by a microbe belonging to the variety called spirochita pallida (appearing under the microscope in the form of flexible spiral filaments). The disease may be acquired by contact with an affected person, or may be inherited from infected parents. Many eye troubles are due to it, the inherited variety causing frequently a deep inflammation of the cornea (interstitial keratitis) and also various affections of the fundus. The acquired variety frequently affects the iris, causing iritis, and may also attack the retina and the choroid.

**Tumours.**

The term tumour, or neoplasm, applies to a localised swelling composed of newly formed tissue which fulfils no physiological function. Tumours tend to grow continuously and independently of the growth of the body. Clinically they can be divided into two main classes, the innocent and the malignant varieties.

Innocent tumours may consist of any of the normal tissues of the body, as bone, muscle, fibrous tissue, etc. They grow slowly, and are generally surrounded by a fibrous capsule. They have no tendency to spread to other portions of the body, but may grow to quite a large size, pushing aside or compressing adjacent organs. They do not generally recur after removal.

Malignant tumours, on the other hand, show a marked departure from the normal structure and arrangement of the tissues of the body. They tend to invade the surrounding parts by sending out prolongations or off-shoots into them, and they frequently spread to other parts, being carried by the blood stream and eventually destroying life. They frequently recur after removal.

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**Death.**

From our brief study of the physiological work of the body we can conclude that the various functions we have investigated constitute the greater part of what are called the vital functions, and so long as these functions are normally performed the body is said to possess life. The cessation of the performance of these functions is what is ordinarily called death.

It should be clearly understood, however, that physiologically there are two kinds of death, namely, local death and general death.

As we have pointed out before, local death is going on at every moment, and in most if not all parts of the living body. We have seen that individual cells of the epidermis of the skin and of all epithelial tissues are constantly dying, and are being cast off to be replaced by others which are constantly coming into separate existence. The same applies to blood corpuscles, and probably to most of the other anatomical elements of the body. This form of local death is insensible to the individual, and is, as a matter of fact, essential to the due maintenance of life.

Occasionally, however, local death occurs on a larger scale as the result of injury or as the consequence of disease. A burn, for instance, may suddenly kill more or less of the skin, or again, a part of the skin may die, as in the case of the slough which lies in the middle of a boil, or again, a whole limb may die and exhibit the curious phenomena of mortification.

As we have seen (page 116) the local death of some tissues is followed by their regeneration. Not only the epidermis and all forms of epithelium, but nerves, connective tissues, bone, and at any rate some muscles, may thus be regenerated even on a large scale. Only, if the dead tissue is highly organised and differentiated for a special function, as is the case for the retina, the regenerated or newly formed tissue is degenerated, i.e., is no longer able to perform the functions of the original tissue. Thus, when a portion of the retina has been killed as a consequence of some disease, the reformed or regenerated portion is made of ordinary fibrous tissue which is quite insensitive to light. Even in the case of the skin, when a large area has been killed by a burn, and the wound extends to the dermis, the reformed tissue or cicatricial tissue differs in appearance from the normal skin, inasmuch as it has a tendency to shrink, so that the edges of the original wound are dragged towards each other, a fact which causes a fair amount of disfigurement.

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Surgeons used to attempt to remedy this by an operation intended to liberate the parts which are brought too close to each other, but now, and as prevention is better than cure, the distortion following a burn is prevented by an operation (grafting) the idea of which originated in the experiment of Garengeot mentioned in page 11. On the part that has been burnt, little bits of sound skin taken from another part of the body or from another person (but not from an animal, since grafting does not succeed from one species to another) are scattered over the destroyed area. These fragments get united to the subjacent part on which, so to speak, they take root; they continue to live and to grow by cell multiplication, so that if the number of these grafted fragments is sufficient, the terrible results due to the retraction of the cicatricial tissue are avoided.

General death is of two kinds, namely, death of the body as a whole, and death of the tissues or anatomical elements. The former term applies to the absolute cessation of the functions of the brain, of the circulatory apparatus, and of the respiratory organs. The latter term applies to the disappearance of the vital actions of the structural anatomical elements constituting the various tissues.

When death takes place the body as a whole dies first, the death of the tissues occurring after an interval which is sometimes considerable, especially in cold-blooded animals. It is a well-known fact that for some little time after what is ordinarily called death, the muscles may be made to contract by the application of a proper stimulus, e.g., an electric current. Again, it is not rare to observe that the hair of a dead man continues to grow for some time. In either case, the muscles and the dermic cells from which the hair grows are not yet dead, though the man himself is dead.

The different ways in which general death is brought about are at first sight extremely varied. We speak of natural death by old age, or by some form of disease, of violent death by the innumerable varieties of injuries or poison, of death by starvation, yet really the immediate cause of death is always the stoppage of the functions of one of three organs, namely, the cerebro-spinal system, the lungs, or the heart. Thus, a man may be instantly killed by an injury to the part of the brain we have called the bulb, as occurs in hanging, or when a person breaks his neck. Or again, death may result from suffocation, i.e., stoppage of the respiratory function by strangulation, smothering or drowning. Finally, death ensues at once when the heart ceases to propel blood. The three organs referred to just now are sometimes called the tripod of life.

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In ultimate analysis, however, life has but two legs to stand upon, the lungs and the heart, for death through the brain is always the result of a secondary action of the injury to that organ upon the lungs and the heart. The functions of the brain cease when either circulation or respiration is at an end, but if circulation and respiration are artificially kept up, the brain may be removed without causing death. On the other hand, if the blood is not oxygenated or ærated its circulation through the working of the heart cannot preserve life, and if circulation is at an end, i.e., if the heart ceases to beat, mere æration of the blood in the lungs is equally ineffectual for the prevention of death.

With the occurrence of general death, the various tissues continue to live for a little while, as we have pointed out before, but they soon die in their turn, and then the every-day forces of the inorganic world no longer remain the servants of the bodily frame as they were during life, but become its master. To quote Huxley, "Oxygen, the slave of the living organism, becomes the lord of the dead body. Atom by atom, the complex molecules of the tissues are broken to pieces, reduced to simpler and more oxidised substances, until all the soft parts are dissipated, chiefly in the form of carbonic acid gas, ammonia, water and soluble salts, and the bones and teeth alone remain. These denser and earthy structures are not, however, competent to offer a permanent resistance to air and water. Sooner or later the animal basis which holds together the earthy salts is decomposed and dissolved, the solid structures become friable and break into powder. Finally, they dissolve and are diffused among the waters of the surface of the globe, just as the gaseous products of decomposition are dissipated through the atmosphere.

It is difficult to follow with any degree of certainty wanderings more varied and more extensive than those imagined by the old philosophers who held the doctrine of transmigration, but the chances are that, sooner or later, some, if not all, of the scattered atoms will be gathered into new forms of life. The sun's rays, acting through the vegetal world, build up some of the wandering molecules of carbonic acid gas, of water, of ammonia and of mineral salts into the fabric of plants. The plants are devoured by animals, animals devour one another, man devours both plants and other animals, and hence it is possible that atoms which at a time formed an integral part of the body and brain of Julius Cæsar may now enter in the composition of Cæsar the negro in Alabama, and of Cæsar the house-dog in an English homestead."

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# CHAPTER VII.

## ACTION OF LIGHT ON LIVING BEINGS. SENSATIONS. GENERAL ARRANGEMENT OF SENSE-ORGANS. EVOLUTION OF THE EYE IN THE ANIMAL WORLD. EMBRYOLOGICAL DEVELOPMENT OF THE HUMAN EYE.

### Action of Light on Living Beings.

Sensibility to light is a general property of the protoplasm of the living cell. Light, i.e., the radiations corresponding to the portion of the spectrum which is visible to the human eye, acts in a great many different ways on living beings. In a general way, we can take it that light produces: (a) Trophic modifications, i.e., modifications in the nutrition and the life of the tissues; (b) Electric phenomena; (c) Visible movements; (d) Sensations and Perceptions.

(a) We cannot say more than a few words on the trophic phenomena due to the action of light. Modern researches have established beyond doubt the fact that light has a strong effect on the low organisms termed microbes or bacteria; it destroys the activity of the poison (toxin) secreted by various disease-producing bacteria. It must be observed, however, that in this respect oxygen plays a part as important as that of light itself, since light is inactive in vacuum. These facts are of the utmost importance from the point of view of hygiene and prove that air and light are absolutely necessary to insure healthy conditions.

If we pass now to higher animal organisms, the influence of light continues to make itself felt; microscopic examination shows that the physiologic activity of the cells of living tissues and the phenomena of cell-multiplication upon which the reproduction of cells and tissues depends, are more marked under the action of light, especially of blue and violet light, as well as under the action of the ultra-violet rays of the spectrum. The excellent results obtained in the treatment of various skin troubles by light (Finsen's method) constitute a proof of the beneficial effect of luminous rays.

Light exerts a considerable effect on the pigmentation of animals; it is easy to observe that in those animals which usually live in illuminated media, the parts of the body that are mainly illuminated (the dorsal part, as a rule) are darker than the parts on which light does not act so directly. In polar regions, white is the dominating shade in the colour

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of animals, and this is probably an effect of the insufficiency of the solar radiation though it may also be a phenomenon of mimicry.

Experiments show clearly the relation of cause to effect between the production of pigment and the action of light. On rearing in the dark animals normally living in ordinary conditions of illumination, they are found to lose their pigmentation. In miners, the skin and even the hair become discoloured in time, even apart from the existence of parasitic anæmia. Conversely, if animals living in dark caves, like Proteus, whose teguments are white or slightly pinkish, are kept under the influence of light, they become coloured first in grey, then in blackish-green, and finally they take a uniform brown coloration. The action of light may be localised in some parts of the body which are illuminated to the exclusion of others. The coloration is due to the formation of pigment which is deposited in the most vascular parts of the skin, and it is clear that the purpose of the newly formed pigment is to protect the skin against the action of luminous rays.

All living beings, from the lowest to the highest, are influenced by the degree of illumination to which they are submitted. We cannot enter deeply into this subject, but a few words on the action of light on the human skin may be of interest. It produces what is termed solar erythema, a condition accompanied by desquamation, pigmentation, and occasionally, blistering. This effect is chiefly due to actinic (or chemical) rays, and may be caused by some artificial light rich in such rays, for instance, the light given by an electric arc-lamp. These chemical rays attack the living cells, and the organism defends itself by a congestion of the capillary vessels of the skin, the blood having the property of absorbing rays of high refrangibility to transform them into rays of lower refrangibility, or calorific rays. A further means of defence is the formation of a layer of pigment; the production of this protective layer may occur under the prolonged action of an insolation insufficient to cause solar erythema. This is shown by the sunburnt complexion of people living mainly in the open air, the peculiar complexion being the result of the defence of the organism against photo-chemical destruction. This character may become hereditary, or fixed, as is the case in the negro race.

(h) The production of electric phenomena in the living tissues, and especially in the retina, under the influence of light is an extremely interesting question, but is somewhat foreign to our present subject; its study belongs to the branch of science concerned with Physiologic Optics.

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(c) The movements produced in living beings under the action of light are very numerous; the phenomenon has been termed photo-motility or heliotropism. Everybody knows the attraction caused by a source of light on many insects: moths get burned in a candle flame, or crowd round an electric lamp. This is an instance of positive heliotropism. On the other hand, some animals seek darkness, and are said to be negatively heliotropic. Heliotropism is not confined to the animal world; plants show it to a marked extent. If a tree is so placed that it can only receive the light from the sun on one side, it will lean in this direction and so orient itself that it may present the greatest possible surface to the action of luminous rays.

Beside the movements of the whole body or the whole organism we have just mentioned, light produces movements in the various tissues, and especially in the retina. When a beam of light is directed to the eye, some of the pigment of the hexagonal epithelium of the retina migrates along the rods and cones whilst, at the same time, there is a shortening of the outer segments of the rods and cones themselves. These movements are relatively slow and, as we shall see in the study of the retina, they are of secondary importance from the point of view of vision, their main purpose being to protect the visual elements (rods and cones) from an excess of light.

(d) The production of sensations and perceptions due to the action of light constitutes the most important part of our subject.

**Sensations. General Arrangement of the Sense-Organs.**

We have pointed out before that the agents by which all the motor organs of the body (except the cilia of some epithelial cells and the amœboid movements of some individual cells like the white blood corpuscles) are set at work are the muscles, made of muscular fibres the essential property of which is their power of contraction, i.e., of shortening, under the influence of an external stimulus.

In the living body any muscle is, as a rule, made to contract by a change in the motor or efferent nerve which is distributed to it. This change, or, as we have termed it, this motor impulse, is generally effected by the activity of a nervous centre (i.e., a mass of grey nervous matter in some part of the central nervous system) with which the motor nerve is connected. The central organ itself is thrown into activity directly or indirectly by the influence of changes which take place in the sensory or afferent nerves which are connected,

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on one hand with the central nervous organ or nervous centre, and on the other hand with some other part, especially the surface of the body. The alteration taking place in the afferent nerve is produced by changes in the condition of the part of the body with which it is connected, changes which usually result from external impressions brought to bear on that part.

Sometimes the central organ enters into a state of activity without our being able to trace this activity to any direct influence of changes in the afferent nerves; the activity seems to originate in the central organ, and the movements to which it gives rise are called "spontaneous" or "involuntary." Putting these cases aside, it may be stated that a movement of the body or of a part of it, is to be regarded as the effect of an influence or, as usually termed, a stimulus, applied directly or indirectly to the ends of afferent nerves and giving rise to a modification of the condition of the particles or molecules of the nerve fibres, i.e., to a nervous impulse, a molecular disturbance which is propagated from molecule to molecule along the fibre to the nervous centre with which the nerve is connected. The molecular activity of the afferent nerve sets up changes of a like order in the cells of the nervous centre and, from these, the disturbance is transmitted along the motor or efferent nerve which passes from the central organ to a certain muscle. When the molecular disturbance travelling in the efferent nerve reaches the ending of the nerve in the muscular fibres, the particles of that fibre are made to take a new position so that each fibre shortens and becomes thicker and a movement ensues. Thus, if we unintentionally prick one of our fingers or touch some very hot object, the hand is jerked away almost before we are aware of what has happened. Such a series of molecular changes as that just described constitutes what we have already alluded to under the name of reflex action, the disturbance or impulse travelling in the afferent nerve and caused by the peripheral irritation being, so to speak, reflected back along the efferent nerve to the muscles.

A reflex action may take place without our knowing anything about it, and, in fact, hundreds of such actions are continually going on in our bodies without our being aware of them. But it frequently happens that we learn that something is going on when a stimulus affects our afferent nerves by having what we call a feeling or a sensation. We classify sensations, together with emotions, volitions and thoughts, under the heading of states of consciousness, though in our present knowledge of physiological and psychological science, we do not really know what consciousness is, and

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how it is that a state of consciousness occurs as the result of the irritation or stimulation of some part or other of our nervous tissue.

**General Sensations.**

Sensations are of various degrees of definiteness; some arise within ourselves, we do not know how and where, and remain vague and undefinable. Such are the sensations of uncomfortableness, of faintness, of fatigue or of restlessness. We cannot assign any particular place to these sensations, which are probably the results of general afferent impulses brought about by the state of the blood or the condition of the tissues. However real these sensations may be, and however largely they enter into the sum of our pleasures and pains, they tell us nothing of the external world; not only are they diffuse, but they are also of a purely subjective nature.

**Special Sensations.**

In the case of other sensations, each feeling arises from changes taking place in a definite part of the body, i.e., is produced by a stimulus applied to that part, and cannot be produced by stimuli to other parts. Thus, the sensations of taste and smell are confined to certain regions of the mucous membrane of the mouth and nasal cavities; those of sight and hearing to the parts of the body called the eye and the ear, and those of touch, though arising over a much wider area than the others, are nevertheless restricted to the skin and to some portions of the membranes lining the cavities of the body. Any portion of the body to which a sensation is thus restricted is called a sense-organ.

It may be remarked that in the case of a sensation of touch, the simple feeling of contact is accompanied by information, not only as to what sense-organ, but also to what part of that sense-organ is being affected. When we touch a hot or a rough body with the tip of a finger, we are aware not only that we are dealing with a hot or a rough body, but also that the body in question is in contact with the tip of the finger; we refer the sensation to that part of the tip of the finger which is acted upon by the body considered. The case is different with other sensations. When we perceive a smell, we know that we smell with the nose, but we do not imagine that the smell arises within the nose; we refer the origin of the sensation to some external cause, namely, to the presence of a smelling body in the vicinity. We even do so when the sensation is due to changes taking place in the nose itself independently of external objects, as

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in the case of the unpleasant odours which accompany certain diseases of the nose. Similarly, our sensations of sight and of hearing are referred to external objects.

In these sensations thus arising in special sense-organs, and hence spoken of as "special sensations," each sensation or feeling results from the action of a particular kind of stimulus to its appropriate sense-organ. In each case the structure of the sense-organ is arranged in such a manner as to render that organ particularly sensitive to its appropriate stimulus. Thus, the sensation of sight is brought about by the action of the vibrations of the luminiferous ether and the eye, or sense-organ of sight, is constructed in such a way that rays of light which, falling on any other part of the body produce no appreciable effect (or at any rate no visual sensation), give rise to vivid sensations when they fall upon it.

In each sense-organ we can distinguish, with more or less completeness, two distinct parts, namely, an essential part and an accessory one. It is through the first that the agent producing the sensation (light vibrations, or sound vibrations, odorous substances or variations in temperature or in pressure) produces changes in certain structures associated with the delicate nerve terminations distributed to the sense-organ. The accessory part, not absolutely necessary to the sense-organ, is useful, inasmuch as it assists in bringing the agent to bear in the most efficient way upon the essential part. In the case of the eye, the accessory part (the dioptric apparatus) is extremely complicated and, indeed, seems to form the greater portion of the sense-organ. In the case of the other senses it is much more simple.

**Sensory Epithelia.**

The essential part of each sense-organ is composed of minute structures which are really modified epithelial cells. The delicate terminations of the nerve filaments distributed to the organ may, with more or less distinctness, be traced to these modified epithelial cells in which indeed they seem to end. These minute structures, these modified epithelial cells, constitute what is termed a sensory epithelium; they serve as intermediaries in each case between the physical agent of the sensation and the sensory nerve. The physical agent is by itself unable to produce in the fibres of the sensory nerve those changes which, on reaching the brain as nervous impulses, give rise to the special sensations. Thus, we know that rays of light falling directly upon the optic nerve itself cannot give rise to a sensation of light; this is shown by the well-known experiment of the blind spot.

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The physical agent must first act on the structures of the sensory epithelium, and these in turn act upon the filaments of the nerve. Thus, light falling on the essential part of the eye (or retina) sets up changes in the modified epithelium cells forming the sensory epithelium; these changes set up corresponding changes or visual impulses in the fibres of the optic nerve which impulses are propagated to the brain and give rise to sensations of light.

Since all our sense-organs are built on the same general principle, and contain an essential part (in the form of a sensory epithelium, the modified cells of which are connected with the fibres of the sensory nerve) and a more or less complicated accessory part, a brief study of the simpler of these organs will help us to understand the working of the most complicated one, namely, the organ of sight.

**Sense-Organ of Touch.**

The sense of touch, which is a sensation of contact or pressure referred to the surface of the body, is located in the skin and the mucous membranes lining the walls of the mouth and nasal passages. In a previous chapter we have pointed out that the skin is not only a protective covering but also an excretory organ which is concerned to a great extent with the regulation of the body heat. At the same time, the skin (and the same applies to the mucous membranes which line those cavities of the body that are in communication with the surrounding atmosphere) is a sense-organ, inasmuch as it is adapted, in some of its parts at any rate, for the reception of impressions due to external stimuli. Cutaneous sensations, i.e., sensations derived from the skin (and mucous membranes) are of various kinds; there are tactile sensations or sensations of touch proper, thermal sensations or sensations of heat and cold, and sensations of pain. An object placed on the palm of the hand may produce a complex sensation involving a sensation of pressure, a sensation of temperature, and, if the pressure be great, a sensation of pain.

The deep layer of the skin or dermis is raised up into a multitude of minute, close set, conical elevations or papillæ, into which sensory nerve fibres are distributed. In those parts where the sense of touch is most acute (tips of the fingers, point of the tongue) the papillæ develop into tactile corpuscles; a tactile corpuscle is a small ovoid body made of delicate connective tissue around which one or more medullated nerve fibres wind two or three times and then, losing their sheaths, the fibre or fibres enter the corpuscle, the axis-cylinders ending in small enlargements.

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It should be understood that no direct contact takes place between the object which is touched and the end of the sensory nerve (papillæ or tactile corpuscles) since the epidermis layer, of varying thickness in different parts of the skin, is always interposed. In fact, if this layer is removed, as when the surface of the skin has been blistered, contact with the raw surface gives rise to a sensation of pain and not to a proper sensation of touch.

Thus, in touch, the essential part of the sense-organ consists of certain structures or epithelial cells very slightly modified in the general skin, and more so in the tactile corpuscles found in those parts of the skin in which the sense of touch is acute; they serve as intermediaries between the physical agent (pressure) and the terminal filaments of the sensory nerves. The accessory part of the sense-organ of touch is very slightly developed, being chiefly constituted by the variable thickness and character of the layers of epidermic cells.

**Various Kinds of Tactile Sensations.**

Tactile sensations proper may be distinguished into: (a) sensations of simple pressure; and (b) sensations of locality.

(a) Mere contact of an object with the skin exerts a pressure on it, resulting in a stimulation by means of which we become aware that something is touching us, and the sensation becomes more acute as the pressure increases up to a certain limit. The sensitiveness of the different parts of the skin in responding to pressure varies, and can be ascertained in a similar way to that in which the sensibility of the retina to light is determined. We can find out the least pressure that can be felt, i.e., the threshold of the sensation of touch; or again, we can determine the least difference of pressure that can be perceived, i.e., the fraction of Fechner. In the first case, small and increasing weights are allowed to press on the skin of the part that is being investigated until a distinct sensation of pressure is felt. In this way, the greatest acuteness of the pressure sense is found on the forehead, the temples and the back of the hand, where a pressure of 2 milligrammes is detected. The skin of the finger tips detects a pressure of 5 to 15 milligrammes. In the second case, when small weights are used, the greatest sensitiveness to differences of pressure is found on the skin of the forehead, the lips and the cheeks, which appreciate a difference of 1-30th of the original pressure. Then comes the back of the last phalanx of the fingers, the palm of the hand and the forearm, which appreciate a difference of 1-15th

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to 1-20th. Small intermittent variations of pressure, as, for instance, in feeling the pulse, are better noted with the tips of the fingers than with the palm of the hand.

Individual sensations of pressure following each other with sufficient rapidity, as is the case if we touch the blunt teeth of a quickly revolving wheel, fuse into one continuous sensation; hence, there is for the sense of pressure something similar to the persistence of retinal impressions.

(b) When an object touches our skin, not only do we experience a sensation of pressure of greater or less intensity, but we are aware of the part that has been touched; this is called the sense of space or locality. Not only is tactile sensibility to a single pressure duller in some parts than in others, a circumstance which may be accounted for by the varying thickness of epidermis interposed between the sensory nerve-ends and the point where the pressure is applied, but the power of distinguishing double or multiple impressions or what we might call the tactile discriminative power is also very different. Thus, if the blunted points of a pair of compasses are separated by only 2 mms., they will be distinctly felt as two if applied to the tips of the fingers, whereas if applied to the back of the hand, only one impression will be felt. This power, which is intimately connected with the sense of locality, depends on the number of sensory nerve-endings in the part considered, for the fewer the nerve-ends in a given area, the more likely it is that the two points will act on only one, and produce but one sensation, and the greater the number of nerve-ends in a given area, the more likely it is that the two points will act on two of them and thus give rise to two distinct sensations.

The table below indicates the least distance at which two points can be separately distinguished:—

| | |
|---|---|
| Tip of tongue ... ... ... ... | 1 mm. |
| Under surface of last phalanx of forefinger ... | 2 mms. |
| Under surface of last phalanx of second finger | 4 mms. |
| Lip ... ... ... ... ... | 4 mms. |
| Tip of the nose ... ... ... ... | 6 mms. |
| Palm of hand ... ... ... ... | 8 to 10 mms. |
| Back of hand ... ... ... ... | 28 mms. |
| Upper part of forearm ... ... ... | 37 mms. |
| Back of neck near occiput ... ... | 40 to 50 mms. |

The power to localise our sensations with reference to the surface of the body, and to indicate the position of the touching object enables the brain to construct a tactile field on the surface of the skin to some part of which the object touching us is referred.



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It follows from what has been said before, and from an examination of the above table, that the touch-corpuscles are unequally distributed over the surface of the body, being numerous and crowded at the tips of the fingers, few and scattered on the arms and the trunk. Our discriminative tactile power, by means of palpation, is in evident relation with this unequal distribution. We can "feel" things better with our finger tips than with any other part of the body, although, as we have seen just now, these have by no means the most sensitive skin. Tactile sensation, though less obviously a special sense than vision or hearing, is different from common sensation, and unless we are on our guard, there is a risk of confusion, owing to the ambiguity of such familiar terms as "feel" and "sensitive." We feel the pulse with the finger tips, but to feel whether it rains or not, we hold our hand palm downwards; if the palm of one hand and the back of the other are exposed together to a slight, gentle drizzle, the droplets may be distinctly felt on the latter, though they are quite imperceptible on the former. We shall see later on that there is a somewhat similar distinction in the case of the retina: the yellow spot, the region in which vision in the ordinary sense of the term, i.e., perception of the shape and details of objects, is most acute, is not the most sensitive part to light.

This fact can be easily ascertained. When an astronomer wishes to see a faint star, he does not direct his telescope (or his own visual axis if the experiment is carried out with the naked eye) onto the star itself, but to a point slightly sideways, in order that the retinal image of the star may be formed on the edge of the macular region instead of being formed on the fovea as is the case in ordinary direct vision. This difference in the sensibility to light of the fovea and of the more peripheral parts of the retina is not astonishing. When a particular kind of cell, like the visual cells of the fovea, is differentiated in view of a special function, that of the perception of the shape of objects in the present case, it loses other functions (in the actual case, the perception of varying degrees of illumination) to a greater or smaller extent.

It is a well-known fact in physiologic optics, that the measurement of the resolving power in any portion of the retina, i.e. the visual acuity, is based upon a principle similar to that which we have described above for the investigation of the tactile sensibility. The method consists in finding the least angular distance at which two luminous points or two luminous parallel lines in space should be placed to give rise to the sensation of two points or two lines

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instead of a single blurred point or a single blurred patch. Experiments carried out by the astronomer Hooke and confirmed later on by other observers, have shown that in order that two points may appear as distinct, they must be at an angular distance of at least one minute, i.e., they must subtend an angle of one minute at the nodal point or optic centre of the eye. It is on this principle that visual acuity charts are built.

It will be noted that the power of tactile discrimination of separate points is most acute in those parts of the body which carry out the widest and most rapid movements. Moistening the skin increases the sensitiveness to separate points, but cold and a bloodless condition of the skin blunts this sensibility. Exercise improves it to some extent, though F. Galton denies the alleged superiority of blind persons in sensitiveness of touch; he argues that the guidance of the blind depends on the multitude of collateral indications to which they learn to give heed rather than on their superiority of touch.

The feeling of warmth or cold is the result of the excitation of sensory nerves distributed in the skin which are probably distinct from those giving rise to the sense of touch. It would appear that the heat (or cold) must be transmitted through the epidermic layer in order to give rise to this sensation for, just as touching an exposed nerve gives rise only to pain, so heating or cooling an exposed nerve or the trunk of a nerve does not produce a sensation of heat or cold, but merely of pain. Thus, if the elbow be dipped into a mixture of ice and salt, the cold first affects the skin and produces a sensation of cold at the elbow, but afterwards it attacks the trunk of the ulnar nerve (which at this point is near the surface of the skin) and this effect is felt as a sensation of pain and not one of cold; beside, the pain thus caused is not felt at the elbow where the cold is acting, but according to a general law, in those parts where the nerve-fibres end, i.e., in the little finger and the ring finger. The sensation of heat or cold is relative rather than absolute. If we put our hand in water as hot as can be borne and then transfer it to tepid water, this feels cold, whereas the same tepid water would feel hot if the hand had been previously kept for a while in ice-cold water.

Like the sense of touch, the sense of temperature varies in delicacy in different parts: the cheeks are very sensitive, more so than the lips; the palm of the hand is more sensitive to heat than its back.

The differences in the sensitiveness of the skin to heat and cold at various points may be readily determined by

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touching the several points with the blunt end of a wire whose temperature can be kept constant at any desired degree. In this way it is found that some points respond to heat but not to cold, others to cold but not to heat, so that we meet with "heat spots" and "cold spots." These spots seldom coincide, nor do they correspond with the points most sensitive to pressure; cold spots are more abundant than heat spots, and the spots are generally arranged in lines, often curved; in some places, heat spots and cold spots partly overlap each other. The arrangement of the cold and heat spots appears to indicate that the nerve-fibres from the two kinds are specifically different.

With regard to the two kinds of temperature sensations and to the general cutaneous surface, it should be noted that the sensations of heat and cold can only be felt through the nerve terminals in the skin; as we have already pointed out, direct stimulation of the nerve, as when the epidermis is removed, only produces a sensation of pain. So also, irritation of the trunk of a nerve by heat or cold not only causes a sensation of heat or cold in the affected part, but it also causes a sensation of pain which, according to a general law, is referred to the peripheral termination of the nerve.

With regard to variations of temperature, it is found that:—

(a) Objects of the same temperature as the part of the skin to which they are applied give rise to no thermal sensations.

(b) The parts of the body having the sense of temperature most acute are, in order: the tip of the tongue, the eyelids, the cheeks, the lips, and the palm of the hand.

(c) Small differences of temperature (about 1° C.) are readily appreciated by the most sensitive parts.

(d) Though the power of the skin to recognise changes of temperature is great, yet our power of estimating absolute temperature by skin sensation is small. Our own feeling of warmth depends on the state of the cutaneous blood-vessels, full vessels leading us to feel hot, and comparatively empty vessels to feel cold; hence an object at the same temperature gives a different sensation according as the skin is full or empty of the warm blood.

(e) Illusions of the sense of temperature are common. A cold weight feels heavier than a warm one; a good conductor, like metal, feels colder than a piece of wood at the same temperature.

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**Sensation of Pain.**

We have already alluded to those vague subjective sensations which arise from a number of sensory impulses proceeding from the skin and other parts of the body, and informing us, in a vague manner, as to our general condition. If these impulses become intense, we have the sensation of pain, so that pain may be regarded as the result of an excessive stimulation of any of the nerve-endings which are concerned in giving rise to sensations.

Pain also results from stimulating the trunks of the nerves leading from these endings to the central nervous system. In this case, the pain is referred to the parts in which the end fibrils of the nerve are distributed. The nerves of any part may thus give rise to pain, and from this it might appear that we can hardly speak of any distinct and separate "sense of pain." There are, however, facts which show that sensations of pain are probably distinct from, though ultimately mixed with, other sensations. Thus, in many diseases of the central nervous system, such as locomotor ataxia, the sensitiveness of the skin to touch may be almost entirely wanting, while pain is readily felt. Further, observation shows that the impulses giving rise to pain pass along the spinal cord on their way to the brain by paths which are distinct from those which convey the impulses resulting from touch or from heat or cold.

From what has been said just now, it appears that the skin contains nerve-fibres of four different kinds, or fibres performing four different functions, namely, pressure, heat, cold, and common sensibility or pain. Whether each of these sets has distinct terminal organs is not definitely known. For the general sensations conveyed by the fibres of common sensibility or pain, no special end-organ for the nerve appears to be needed, since we know that pain can be produced by stimulating, i.e., pinching, heating, etc., the open surface of a wound or the cutaneous nerves themselves. But such stimulation gives no sensation of pressure or heat, only pain, and this suggests that there must be some special mode of ending for the nerve-fibres carrying sensations of pressure, heat and cold.

**The Muscular Sense.**

The muscular sense is less vaguely localised than the subjective sensations we have examined, though its exact location is not accurately defined. What is called a muscular sensation is the feeling of resistance which arises when any kind of obstacle is opposed to the movement of the body or of any part of it; it is something quite different

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from the feeling of contact or that of pressure. If we lay our hand flat on its back upon a table and rest a disc of cardboard upon the ends of the outstretched fingers, the only result will be a sensation of contact, the pressure of so light an object being inappreciable. If now, we put a two-pound weight upon the cardboard, the sensation of contact will pass into what appears to be a very different feeling, namely, that of pressure. Let now the hand be raised from the table; another feeling, that of resistance to effort, will make its appearance. This feeling comes into existence with the exertion of the muscles which raise the arm, and it is the consciousness of this exertion which goes by the name of muscular sense.

Anyone who raises or carries a weight knows well enough that he has this sensation though he may be puzzled to say where he has it. Nevertheless, the sense itself is very delicate, and enables us to form tolerably accurate judgments of the relative intensity of resistances. Persons who deal in articles sold by weight are able, by constant practice, to form very precise estimates of the weight of such articles by balancing them in their hands, and in doing this, they depend in a great measure upon their muscular sense.

The muscular sense embraces more than the mere consciousness of the resistance to effort involved in the act of lifting a weight. Thus, it is a matter within everybody's experience that, even when the eyes are closed, we are well aware of the direction and extent of any movement of any part of the body. Moreover, we are equally conscious of the position of any part of the body at any moment, whether the position is the result of our own voluntary movement or the result of the action of some other person who has placed the part in its actual position. In all such cases the muscular sense supplies the basis of our knowledge of the position or of the movements of the parts of our body.

The muscular sense contributes largely to our knowledge of the external world. Though the muscular feelings are rather difficult to localise, they are delicate and enable us to discriminate slight differences in the range and force of movements. Muscular movements are an important factor in acquiring a knowledge of the space relations between things generally, though how the muscles help in these space-perceptions, whether by their own sensations or by awakening sensations of motion in the skin, retina and articular surfaces, is still undecided. It is in combination with other senses that the muscular sense plays its most important part, for, in almost all sensations, muscular sensations form an element. In listening, the muscles of the

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ear-drum contract and the head is moved in the direction of the sound. The delicacy of the sense of touch stands in a definite relation to the mobility of the different parts of the body, those parts being most mobile which are most delicate of touch. Combined with tactile sensations, muscular sensations give rise to composite sensations which enable us to estimate small differences of weight and small amounts of resistance, and also render possible the knowledge and relations of the parts of surfaces and solids that enter into the idea of form.

The muscular sense plays an important part in the work of the eyes. We ascertain the distance of near objects in terms of the amount of convergence, i.e., of the muscular work we have to exert to bring the two visual axes to bear on the object looked at. Likewise, we estimate, to a certain extent, the length and width of objects by the amount of muscular effort we have to exert to cause our visual axes to move along the length or width of the object under examination. In a general way, the changes in the visual field due to the rotation of the eyes under the action of the extra-ocular muscles aid us in the building up of our complex ideas of the objects in the external world.

**The Nervous Mechanism of Sense-Organs Generally.**

In a general way, all sense-organs consist essentially of a peripheral neuron connected, either directly or through intermediate neurons, with the cells of the portion of the brain cortex concerned with the perception of touch, or of smell, or of taste, or of sound, or of light.

Let us take as example the sense of smell. The external part of the mucous membrane of the nose is constituted by an epithelium in which certain cells are differentiated and assume the form of nervous bipolar cells. Their protoplasmic or dendritic processes are very short and slightly project over the surface of the mucous membrane so as to receive directly the stimulation produced by currents of air laden with smelling particles which pass into the nasal cavities. The axons or cylinder-axes of the cells are grouped so as to form a nervous trunk which ultimately reaches the cells of the portion of the cortex concerned with the perception or sensation of smell.

In more complicated sense-organs the main arrangement remains the same, but intermediate neurons are intercalated on the path of the impulses. In other words, a sense-organ consists essentially of a peripheral neuron, the protoplasmic or dendritic processes of which are directly exposed to the stimulation of some external agent (smelling

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particle, or sound waves or light waves), and of a central neuron in the brain in which the stimulations are received and converted into sensations. These two neurons may be connected together by a variable number of intermediate neurons which form a continuous path along which impulses travel from the peripheral to the central neuron.

As a general rule, the nervous cell forming the cellular body of any neuron receives its stimulation by its protoplasmic or dendritic processes, which are cellulipetal, and transmits it to the protoplasmic or dendritic processes of the next neuron by its axon or cylinder-axis, which is then cellulifugal.

All peripheral sensitive neurons do not react to the same stimulus. According to the kind of stimulus to which they react the various sense-organs are classified under the five main headings:—

(1) The protoplasmic processes of certain neurons are distributed into the skin and, as we have seen just now, they have the property of reacting to mechanical pressure and to heat or cold, etc. They enable us to perceive the form, the dimension, and the temperature of external bodies by simple contact. The skin is therefore the seat of the sense of touch, or of tactile sensibility.

(2) The dendritic processes of other neurons are distributed to the surface of the tongue; they have the property of being stimulated by liquids, or by substances capable of being dissolved by the saliva, and enable us to perceive the taste of these substances. The tongue is thus the seat of the organ of taste, or of gustative sensibility.

(3) Other peripheral neuron have their protoplasmic processes on the surface of the mucous membrane of the nose, as we have seen just now, and these processes are stimulated by gaseous substances, or by air laden with particles of smelling matter; the nose is, therefore, the sense-organ concerned with the perception of smell, the organ of olfaction.

(4) In the ear we have again a peripheral neuron, the dendrites of which are stimulated by sound waves, and the axons constitute the acoustic nerve. This arrangement constitutes the nervous part of the organ of hearing.

(5) Finally, in the eye, the protoplasmic processes of the visual cells of the retina are particularly adapted to the stimulus produced by light waves or light rays, as we shall see much more fully at a later stage.

In the case of the organ of hearing, and that of the organ of sight, the purely nervous apparatus is accompanied

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by other parts which, though they are not directly concerned with the perception of sound or that of light, yet enable the proper stimulus produced by sound waves or light waves to be utilised to the best advantage. In one of the next chapters we shall deal with these parts, at least as far as the organ of sight is concerned.

**Evolution of the Eye in the Animal World.**

A definition of the eye is somewhat difficult to give considering the numerous variations of form the organs of sight assume in the zoological scale. As we have already stated, the lowest types of living beings are unicellular, and light reacts on the protoplasm of the cell in a vague and confused manner, determining in it various movements and reactions which, of course, cannot be regarded as constituting a sense of vision. A little higher in the scale, we find that some portion of the protoplasm tends to become differentiated or specialised in view of the formation of a rudimentary organ with a new function; thus, in pluricellular animals, the simplest visual organ or eye-spot is formed by certain cells of the ectoderm or covering surface, the protoplasm of which becomes loaded with pigment; here again, there is no vision in the usual sense of the term, but if we continue to ascend the zoological scale, we soon find that the nervous system appears with its special function of collecting, controlling and centralising the most various forms of stimulation received from the external world, and especially we see the apparition of an organ intended to receive the impressions produced by light. This organ is connected by a conductor or nervous fibre to the nervous centres. Such are the unicellular eyes of many worms and of some of the lower types of molluscs. It is clear that this isolated element, this elementary eye, cannot give anything more than a mere quantitative or perhaps a qualitative notion of light. In order that a notion of the direction followed by luminous rays may be obtained, it is necessary that similar elements may become grouped so as to form a convex surface—this brings us to the compound eye of arthropodes (insects, spiders, etc.).

**The Compound Eye of Insects.**

The eye of the domestic fly consists of a hemispherical convex faceted surface, and dissection shows that the organ is a collection of conical elements, each of which is an elementary eye or ommatide, built on the type of the simple eye of worms, but with a higher degree of perfection. Thus, the external facet of each ommatide is transparent and may

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be regarded as a cornea; behind it there is a transparent cylindrical or more exactly conical rod of highly refracting material which corresponds to the crystalline lens of the human eye, and is termed the crystallinian cone. A membrane or retinula receives the posterior end of the crystalline cone and a nervous fibre connects this membrane with the optic ganglia or nervous centres. Each elementary eye or ommatide is separated from the neighbouring ones by sheaths of pigment. The purpose of each ommatide is evidently to collect the luminous rays proceeding from objects in various directions. This is ascertained by a microscopic examination of the posterior end of a compound eye when the corneal facets are directed towards various sources of light; it is then seen that the retinula of each ommatide is occupied by a luminous spot which is a minuscule image of the source of light towards which the ommatide is directed. It follows that a compound eye gives an erect image of the surrounding space.

If we consider that in many instances the refracting apparatus must work both in air and under water, as is the case for amphibious arthropodes, it is logical to attach but little importance, from the optical point of view, to the curvature of the outside or corneal surface, and to assume that the refracting power is entirely or almost entirely due to the crystallinian cone. An examination of this structure with the microrefractometer shows that it is not optically homogeneous, but is made of concentric lamine, the refractive index of which is maximum along the axis of the cone and decreases gradually as the surrounding pigmented sheath is approached. It can easily be seen that such a structure acts somewhat like a convergent lens, the converging effect being due to the variation in the indices of the concentric layers instead of being produced by the curvature of the refracting surface, as is the case in lenses.

These considerations show that the compound eye as found in insects, spiders, etc., derives from a primitive type, namely, the pigment spot of worms; this pigment spot is convex and so is the external or corneal surface of the compound eye, since this surface is made of a collection of convex elementary eyes. For this reason, the compound eye of arthropodes is termed an extrorse eye.

Up to now we have seen that the evolution of the eye consists of two main stages. In the first stage, represented by the pigment spot, the element sensitive to light is isolated. An eye of this sort can only provide a quantitative and perhaps a qualitative notion of illumination, but not anything comparable to vision as we understand the expression.

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In the second stage, represented by the compound eye, the various components are so grouped as to project onto the sensitive membrane a rough erect image of surrounding objects.

**The Eye of Molluscs.**

In the third stage, we find a more perfect type characterised by the fact that the sensitive membrane forms a concave surface on which a dioptric apparatus projects an inverted image of external objects. Exactly as the compound extrorse eye of arthropodes derives from the convex pigment spot, the more perfect eye of higher animals and man derives from the hollow or concave eye-spot found in the lowest types of molluscs. All the steps in the progressive development are met with at some part of the zoological scale. The small concave depression becomes enlarged and the edge of the cup-like structure narrows until we have a hollow cavity presenting a small opening or pore through which luminous rays may enter. Thus, in the case of the Nautilus, a mollusc of the lowest type, the eye is comparable in all respects to a pinhole camera; an image of external objects is projected in it with a relative sharpness, but the luminosity or brightness of this image is obviously slight. The closing of the cup by a transparent membrane and the adjunction of a refracting medium constitute the next improvements, and have the effect of notably increasing the sharpness of the image. At the same time, the pore or aperture through which light is admitted is enlarged, a fact favourable to a greater brightness, without a loss of sharpness. The eye of the common snail is built on this principle. It is a globe, approximately spherical, enclosed in a resisting envelope or sclerotic, perforated by a hole through which the optic nerve enters. At the opposite pole the sclerotic is transferred into a transparent cornea. The central cavity is occupied by a transparent body playing the part of the refracting media of the human eye. The retina is made of rod-like cells between which pigment cells are arranged.

**The Eye of Mammals.**

It is from the type described just now that the human eye is derived by gradual improvements, consisting in the formation of a crystalline lens separated from the medium filling the greater part of the ocular cavity, in the formation of an anterior chamber filled with aqueous fluid, and in the development of the iris diaphragm. In the lower types of vertebrate animals the crystalline lens is movable bodily, a feature intended to adapt vision to different distances,

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whereas in the higher types, this same adaptation to various distances, or accommodation, is secured by alteration in the curvature of the crystalline lens under the action of a special muscle termed the ciliary muscle.

**Production of Light by Living Beings.**

To conclude this brief survey of the effect of light on various organisms, a few words on the production of light by living beings may be of interest. Man found such difficulties in first obtaining fire and its twin-brother light that old legends will have it that a mortal stole it from heaven. Yet numberless creatures belonging to species descending lower and lower in the scale of life can both generate and radiate light. By means of the light thus radiated, either from their bodies generally or from special organs, they can illuminate the medium in which they live.

A great many bacteria included in the genus Photobacterium, present the photogenic function, i.e., the faculty of emitting light, to a fairly high degree. It is to bacteria of this kind that the phosphorescence of some fishes is due. In these low organisms the photogenic function is diffused in the cellular protoplasm, but on ascending the scale we find that the function becomes located in some special organs. Many crustaceans are luminous, having on various parts of the body some luminous globules or photospheres which are sometimes fitted with reflectors and lenses, and have been mistaken for eyes.

Of all animals, insects are those which exhibit the photogenic faculty to the greatest extent. The best known amongst luminous insects are the glow-worm (Lampyre noctiluque) the luciole and the pyrophore, commonly called Cucujo by natives of West Indies. In the glow-worm, the luminous apparatus consists of two small yellowish spheroidal masses on each side of the posterior part of the body. In the pyrophore there are three lamps, two are symmetrically placed on each side of the head near the junction of the head and the thorax; the third is on the lower part of the body, in the middle line, and cannot be seen when the insect is at rest on the ground. When the three lamps are in action, the light given by the third one is brighter than that given by the other two acting together.

The illuminating power of one of the pyrophore's side-lamps is estimated to be 1-150th of a candle, and the pair of lamps, when brought about 30 cms. from fine print, permit the print to be read.

The light emitted by the pyrophore and the glow-worm has been investigated by means of the spectroscope, which

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shows that the spectrum it produces is continuous, without dark lines, and extends from the line B to the line F; this means that the radiations the mixture of which constitutes the light emitted by the animal contain a little less red and considerably less violet than ordinary solar light; in fact the violet is hardly visible in the spectrum of the pyrophore light and this explains, no doubt, the weak actinic or chemical action of this light. An exposure of at least five minutes has been necessary to obtain the photograph of an object illuminated by the light of a pyrophore, the plate used being of such a sensibility that an image equally intense could be obtained in a fraction of a second when the same object was illuminated by ordinary daylight.

The calorific power of the light emitted by luminous insects is infinitesimal as compared with that of our ordinary sources of light; whereas with our usual sources of light about 96 to 98 per cent. of the energy spent to produce light is transformed into heat which we do not want, and only 4 or 2 per cent. is transformed into the light we do want, in the case of the pyrophore light, the figures are exactly reversed, about 98 per cent. of the energy spent by the animal to excite its lamps being transformed in light, and 2 per cent. only in heat. Such a light is termed a cold light, and it is only when the production of a light of this sort is possible industrially that the problem of illumination will be solved on an economical basis.

Amongst the higher animals, the photogenic function is only observed in those fishes which live in abyssal depths far beyond the reach of the remotest rays of sunlight. The reader who may be interested in the subject will find fuller information in a lecture delivered by the author at a meeting of the Optical Society on November 14th, 1912. This lecture is reproduced verbatim in the Transactions of the Optical Society (Vol. XIII. pages 34-62), and in *The Optician* (November and December, 1912).

**The Embryological Development of the Eye. The Optic Vesicles.**

As we have already pointed out (page 17), every living creature starts life from a single cell, i.e., from a minute corpuscle of living substance or protoplasm in the mass of which a tiny body or nucleus is embedded; this cell or ovum, after it has been fertilised, lives and grows for a certain period, then it divides itself into two halves, each of which gradually assumes the size and shape of the parent cell. These two in their turn divide, giving rise to four, and so on. This process goes on until the embryo is an aggregate of numerous nucleated cells similar to each

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other. Then, the cells arrange themselves in three layers, the outermost being called the epiblast or ectoderm, the innermost the hypoblast or endoderm, and the middle one the mesoblast or mesoderm.

From these three fundamental embryological layers, all the tissues and organs of the adult are formed. In this process of development there is not only cell multiplication, but the original cells which were undifferentiated, i.e., all similar to each other, become changed into groups of differentiated cells, the cells of each one group being like each other but unlike those of other groups. Eact set of differentiated cells constitutes a tissue and each tissue is variously distributed amongst the different organs, each organ generally consisting of more than one tissue. Some cells become thin and flat, and, cohering at their edges, form the blood-vessels; others become elongated and thread-like to form the fibres of the muscular and nervous tissue; others become separated by intercellular substance derived from the cells themselves and in this intercellular substance, fibres such as are found in connective tissue may arise or calcareous matter is deposited as in bone.

From the three embryological layers mentioned above, all the tissues and organs of the adult are formed, the cells multiplying by division, as we have explained, and the different structures being developed either by outgrowth of existing parts or by involution or invagination, i.e., folding in of existing parts. From the ectoderm the epidermis or outside covering of the body, the nervous system and the nervous apparatus of the sense-organs are formed. The endoderm forms the respiratory and the digestive system and the mesoderm, the blood corpuscles, the connective tissue, the bones and the muscles of the body.

At an early stage in the development of the embryo a folding of its cells takes place so that the upper embryonic area assumes the character of a groove termed the medullary or neural groove (see fig. 10). As growth proceeds and the cells continue to multiply, the two edges of the groove approximate and ultimately fuse together; the effect of this is to transform what was the neural groove into the medullary or neural canal which is destined to become the central canal of the spinal cord, and the cavities of the brain known as ventricles. The walls of the neural canal are composed of cells of the ectodermic layer, and it is from these cells that the whole central nervous system as well as the most important parts of the nervous apparatus of the eye will be formed.

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The hinder or posterior part of the canal is narrower than the anterior portion. This posterior part is that which gives rise later on to the spinal cord, whereas the front or anterior part is concerned with the development of the brain itself. Here, at an early stage, two very obvious constrictions appear in the region of what is to be the brain. These constrictions divide the brain into three distinct parts or vesicles, as we have explained before, and as shown diagrammatically in fig. 11. A part of the posterior vesicle ultimately develops into the cerebellum or little brain, the other part forming the medulla oblongata or hind brain in which lie so many of the centres of nervous energy. The central vesicle formed by the constrictions will form what is known as the middle brain. The foremost or anterior cerebral vesicle is of the greatest importance from our point of view, since it is from it that the great mass of the cerebral hemispheres or cerebrum is developed together with various outgrowths, amongst which is the nervous apparatus of the eye.

If we follow the development of the embryo brain from an early stage, we soon see a couple of hollow pear-shaped vesicles which spring from the foremost part of the first or anterior cerebral vesicle; these growths are the primary optic vesicles; they are at first directed outwards and forwards, but presently grow downwards and ultimately reach the outer covering of the body, i.e., the outer ectoderm in the part in which the eye will ultimately be. A remarkable change then occurs; the portion of the optic vesicle remote from the brain gradually flattens, then becomes concave, and finally penetrates into the portion of the vesicle near to the brain, this invagination giving rise to a kind of cup formed of two layers applied over each other just as one might form a cup in a blown paper bag by forcibly pressing one portion of it into the other. The cup-like structure thus formed is the secondary optic vesicle; it differs from the primary optic vesicle in the fact that its wall is made of two laminæ, the internal one representing the distal part of the primary vesicle, the part remote from the brain; this internal layer will give rise to the retina proper, whereas the external one, representing the proximal part of the vesicle, the part near to the brain, will form the pigment epithelium of the retina. (See figs. 15, 16 and 17.)

Thus the retina proper is developed at the expense of the internal layer of the secondary optic vesicle, which itself represents an island of the wall of the neural canal derived from the ectoderm. This fact is of importance since, as we shall see presently, it explains the inversion of the retina.

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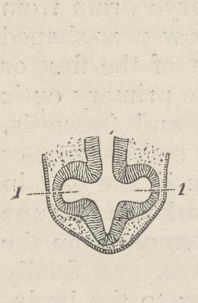
**The Formation of the Lens.**

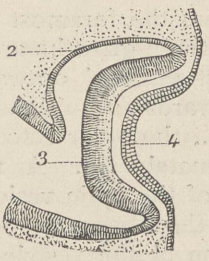
At the point where the secondary optic vesicle comes into direct contact with the outside covering there occurs a thickening and a depression of this covering; the pit thus formed, the lens pit, is converted into a closed sac or lens vesicle, the thick edges of the pit joining together. Later on the lens sac severs itself entirely from the horny plate, its source of origin. The hollow of the sac is afterwards filled by multiplication of the cells of its thick walls, and thus we get the solid crystalline lens, which is of purely ectodermic origin.

At first the lens lies directly on the invaginated part of the secondary part of the secondary optic vesicle, but the two structures soon become separated, a new part, of mesodermic nature, growing between them. Finally, a complete fibrous envelope, also of mesodermic origin, is formed about the whole of the organ and its stem or optic nerve; it originates from the part of the head plate which immediately surrounds the eye. This envelope takes the form of a closed



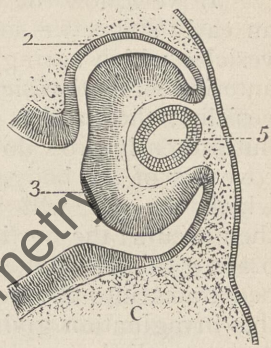

A

FIG. 15.




B

FIG. 16.




C

FIG. 17.

FIGS. 15, 16 and 17 illustrate three different stages in the development of the eye in the human embryo. FIG. 15 shows the development of the primary optic vesicles, in the form of pear-shaped hollow bodies, *1–1*, which spring from the lateral parts of the anterior cerebral vesicle and push their way outwards toward the part of the head where the eye will ultimately be, remaining attached to the cerebral vesicle by a stem which will become the optic nerve. While the primary vesicle thus moves towards the ultimate position of the eye, its external wall thickens, then flattens and finally is pushed inwards so as to form what is called the secondary optic vesicle, shown in 2 and 3 in FIGS. 16 and 17. From the lamina 2 of the cup-like structure represented by the secondary optic vesicle, the pigment epithelium layer of the retina will be formed while the invaginated lamina 3 will develop into the retina proper.

In FIG. 16, 4 represents the external or ectodermic layer in what will be the head of the embryo. This layer gradually hollows and thickens by proliferation of its cells in the part just opposite the secondary optic vesicle; the central part of it thus forming the lens pit. A further development of it gives rise to the embryo crystalline lens which at first remains attached to the outer ectoderm but ultimately separates from it to constitute the lens as shown at 5 in FIG. 17.

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round vesicle surrounding the ball and pushing its way between the lens and the front plate; the wall of this capsule soon divides into two different membranes by surface cleavage, the inner lamina becoming the uveal membrane (choroid, ciliary body, and iris) and the outer one being converted into the outside protective coat of the eye, namely, the sclerotic and the cornea.

The eye is now formed in all its essential parts. Let us revert to some important points in the development of the eyeball. We have seen just now that the lens, which develops from the ectoderm of the outside covering of the body, fills at first the cavity formed by the invagination of the optic vesicle, as there is yet no vitreous to separate the retina from the crystalline lens. The vitreous develops from the mesodermic plate, which pushes its way between the inner lamina of the secondary optic vesicle and the lens.

**The Fœtal Cleft.**

Even as early as the time when the primary optic vesicle is undergoing invagination to form the cup-like structure we have termed the secondary optic vesicle, we notice that in the region of its lower side the wall of the cup is altogether deficient. Here, then, an infolding exists in the wall of the cup, a feature which is continued backwards in the stem of the optic vesicle (i.e., in what will be the optic nerve) in the form of a furrow (fig. 18). It is through

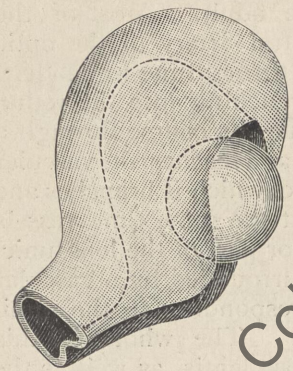

FIG. 18 (after Hertwig) shows diagrammatically that the fœtal cleft results from the same mechanism as that of the formation of the secondary optic vesicle, i.e., by folding in of the anterior part of the vesicle. This cleft, wide at first during the early periods of development, gradually narrows by approximation of its edges so that what we might call the primitive ocular globe assumes the form of a spheroid body attached posteriorly to the brain vesicle by the optic stem and hollowed anteriorly to lodge the embryo crystalline lens.

this fissure or fœtal or ocular cleft that vessels, together with mesodermic tissue, gradually grow from the outside into the interior of the eye, pushing a way between the retina and the lens. The cleft becomes closed when the development of the eye is complete, though, as we shall see later on, it may happen that, owing to an arrest of development, the closure does not take place and a gap is



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left either in the optic nerve or in the globe, constituting what we shall study under the name of Coloboma.

At this early stage the lens which has budded from the ectodermic covering of the body lies in direct contact with this covering. Then, mesodermic tissue grows in from all sides at the anterior margin of the ocular cup between ectoderm and lens. In this mass of mesodermic tissue, there afterwards develops a slit which becomes the anterior chamber; the portion of mesoderm lying in front of the slit forms the cornea, the portion behind it forms the iris. At the same time as the mesoderm grows to form the cornea and iris, it also develops to enclose the whole of the posterior part of the eye, and this envelope later on splits into two separate structures, the sclerotic outside and the uveal tract inside.

Thus at first the sheath of mesodermic tissue which surrounds the secondary optic vesicle is made of round cells and no differentiation can be made between the outer coat of the eye (sclero-corneal coat) and the uveal membrane. Later on the inner part becomes vascularised and the two coats become distinct; pigment does not form in the choroid until the seventh month of fœtal life and sometimes later. The stroma of the iris is not pigmented at birth, the pigmentation taking place gradually and being completed about the end of the first year of separate life.

The arrangement of the vessels in the embryo eye is different from that observed in the adult. Most of the internal vessels derive from the central artery of the optic nerve, which has been able to pass in through the fœtal cleft, and this artery, instead of merely branching into the retina as is the case in the adult eye, continues its course through a canal in the vitreous (canal of Cloquet) and reaches the vascular tunic of the lens in the posterior part of which it branches and ramifies up to the circumference. At the same time vessels derived from it pass on into the anterior part of the lens tunic. Thus, the lens of the embryo eye is surrounded by a vascular membrane which in the portion corresponding to the pupil is termed the pupillary membrane. The whole of this vascular membrane, or tunica vasculosa lentis, as well as the hyaloid artery, disappears about two months before birth, but occasionally scattered remnants of the pupillary membrane or of the hyaloid artery are found in new-born infants. As the central artery of the retina passes into the canal of Cloquet, branches are distributed in the peripheral portions of the vitreous body; these vessels also disappear shortly before birth.

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The vessels of the retina develop by branching off from the central artery of the optic nerve at the nerve entrance and push on into the layer of the optic nerve fibres of the retina while the vessels of the vitreous, previously present, undergo obliteration.

**General Considerations on the Embryological Development of the Eye.**

The main point to bear in mind in this brief study of the development of the visual organ is the circumstance that the optic nerve, the retina and its pigment epithelium originate from an outgrowth of the brain, while the lens develops from the outer covering. The delicate conjunctiva which afterwards covers the outer surface of the globe also derives from the external layer of the embryo. The lachrymal glands are ramified growths from the conjunctiva. All these important parts of the eye are products of the outer or ectodermic embryological layers; the remaining parts, the vitreous, the choroidal or uveal coat, and the sclero-corneal envelope, are mesodermic formations. The outer protection of the eye, the eyelids, are merely folds of the skin.

To sum up, in vertebrates the eye is mainly a part of the brain which has grown forwards towards the skin, and not merely a direct derivation of the covering envelopes of the embryo as is generally the case in invertebrate animals.

We have already pointed out the fact that the retina of vertebrate animals is inverted, that is, that the sensitive layer is most remote from the optic system; it follows that luminous rays have to pass through all the retinal layers before they can reach the sensitive one. This disposition is different from that presented by other sense-organs in which the sensitive part usually faces the medium from which it receives impressions. The inversion of the retina is neither a physical nor a physiological necessity, since there exist non-inverted retinæ; such is the case, as we have seen, in the retina of many invertebrates, molluscs, for instance, and also in the pineal eye of some reptiles, about which we shall say a few words presently.

The peculiar situation of the sensitive layer in the retina of invertebrates finds its explanation in the development of the retina and in the origin of the part of the brain from which it derives. It results from the researches of modern anatomists that only the ectodermic layer of the embryo, that is, the layer the cells of which are directly related to the surrounding medium, is capable of giving rise to the sensitive part of the sense-organs, or, as sometimes termed, to a sensory epithelium. When the ectoderm of the embryo brain has become invaginated on the dorsal line to form first

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the neural groove, and later on the neural canal, the ectodermic surface becomes the internal surface of the canal; it is this surface, and this surface only, which, owing to its origin, is apt to give rise to the sensory cells of the retina.

It must be borne in mind that the retina is developed at the expense of the internal layer of the secondary optic vesicle; the posterior surface of this layer corresponds to the primitive ectodermic surface; it is therefore this surface which is capable of forming the sensitive layer. In other words, we can say that the visual cells occupy the posterior surface of the retina because this surface is a derivation of the primitive ectodermic surface, origin of all sensorial cells.

**The Pineal Eye.**

We have alluded just now to the pineal eye. In the embryo brain of a vertebrate, the portion of the brain (anterior cerebral vesicle) from which the primary optic vesicle springs presents, at its upper part, a hollow diverticulum; this structure, which is called the epiphysis, resembles very closely the primary optic vesicle. In birds and mammals the epiphysis of the embryo becomes atrophied in the adult stage and forms what is known as the pineal gland. In some reptiles and amphibians, however, the epiphysis develops like the primary optic vesicle and, reaching the surface of the skull at a point corresponding to a hole in the bone termed the parietal hole, forms a kind of more or less complete eye, generally hidden under the skin.

The parietal hole is well marked in the fossil amphibians of the Jurassic and Cretaceous periods, Ichthyosaurus, Plesiosaurus, etc., and it is not improbable that the pineal eye of these extinct species was a well-formed and useful organ at the time these animals flourished.

In most animals of the present period in which the pineal eye exists (Gecko, Chameleon, Iguana, etc.), this organ is in a condition of arrested development and is not capable of performing the visual function, but in Hatteria Punctata, a lizard found in New Zealand, it presents a comparatively high degree of perfection, though even then it does not seem to serve a useful purpose.

The pineal eye of Hatteria is formed of a closed vesicle surrounded by a capsule of connective tissue. It is immediately below the parietal hole, and the skin covering the hole is deprived of pigment; the anterior part of the ocular vesicle is thickened to form a crystalline lens of cellular nature; the posterior part is occupied by the retina, to the middle of which a stem corresponding to the optic nerve is attached.

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The development of this eye is easy to understand. The epiphysis pushes its way upwards, and, reaching the skin, becomes transformed into an eye by simple modification. The distal part of the vesicle thickens into the crystalline lens and the proximal part forms the retina, which is thus continuous with the lens at its edge, the two structures having the same ectodermic origin; the hollow peduncle of the epiphysis becomes the optic nerve.

The layer of visual cells of the retina occupies the anterior surface of the membrane, which corresponds to the internal surface of the embryo brain. Though the retina of the pineal eye derives from a kind of cerebral vesicle, it is not inverted because there has been no invagination, no formation of a secondary optic vesicle.

In Lacerta Ocellata, the pineal eye is built on the same principle, but symptoms of degeneration are apparent in the cells of the retina. In the chameleon, the pineal organ remains at a rudimentary stage. In many fishes and reptiles as well as in all birds and mammals, including man, the epiphysis does not reach the skin; the atrophy is complete, all that is left of it being the pineal gland, a small reddish body, about the size of a cherry stone in the case of a man.

**Main Points of Difference in the Development of the Eye in Invertebrate and in Vertebrate Animals.**

From these considerations and from what has been said in the previous pages on the development of the eye, it is clear that the visual organs derive from the ectoderm, either directly by differentiation of the outside covering of the body or indirectly at the expense of the anterior part of the embryo brain. The mesoderm intervenes in an accessory way, and the endoderm does not take any part in the formation of the eye.

The eye-spots found in the lowest type of the invertebrates are of an exclusive and direct ectodermic origin. The compound eye of arthropodes is developed from the hypodermic layer of the outside tegument; the cells of this layer become transformed into groups of cylinders perpendicular to the membrane from which they derive. Then, each cylinder is divided transversely into two parts, an external one which will give rise to the crystalline cells and to the pigment cells, and an internal one which will produce the visual and the pigmentary retinal cells. From the crystalline cell the cuticle and the crystalline cone will be formed later on.

The eyes of the lowest molluscs are also developed from a pit-like depression in the outside tegument; the narrow

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orifice of the pit may remain open so as to communicate with the aqueous medium in which the animal lives, as occurs in the case of the nautilus, or it may become obliterated so as to form a closed vesicle as in the case of gasteropode molluscs. In cephalopode molluscs, the eye, fitted with a true crystalline lens, is formed in a similar way; the crystalline lens being made of two portions, the anterior one derived from the ectodermic covering, the posterior one from the closed vesicle.

The eye of vertebrate animals belongs to the indirect ectodermic type. The pineal eye of lizards, which only exists in a rudimentary state in the actual species, derives from the epiphysis, a hollow diverticulum proceeding from the upper part of the primary anterior brain, which pushes its way until it comes into contact with the outside skin at the level of the parietal hole; this pouch-like diverticulum is then transformed into an eye by simple modifications; its distal part thickens so as to form a transparent lens, while the proximal part becomes the retina, the rods of which are directed forwards as is the case in the retina of molluscs, and are surrounded by pigment sheaths. A fibrous capsule, of mesodermic origin, forms the sclero-corneal coat.

The development of the lateral eye of vertebrates is the result of three different formations: the optic vesicle, a cerebral product of the ectoderm, forms the retina proper and the pigment epithelium; the outside ectoderm forms the crystalline lens; and the mesoderm forms the uveal membrane and the sclero-corneal envelope.

These considerations are sufficient to give an idea of the general development of the visual organ. When we study the various coats and refracting media, we shall examine with more detail the peculiarities of structure of each of these parts.

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# CHAPTER VIII.

## THE EYEBALL GENERALLY. THE SCLERO-CORNEAL COAT.

**The Eyeball.**

As a general rule, the eyes of vertebrate animals and those of the human being are two in number, and usually occupy symmetrical positions in the head with respect to the sagittal plane of the body. There are exceptions to this rule, as, for instance, in the type of fishes (turbot, sole, plaice), the body of which is flattened from side to side instead of from above downwards as is the case for the majority of other fishes. In such animals, which swim on their side, the eyes are on the side of the body which is oriented upwards. This arrangement is secondary to the mode of life of the animal; the embryo has symmetrical eyes, and it is but at a relatively advanced stage of development that one eye has become displaced by a rotation about the longitudinal axis of the body till it comes close to the other eye. The fully developed fish of this kind has thus a blind side directed downwards, and an upper side possessing two eyes.

We need not insist on such peculiarities since we are mainly concerned at present with the human eye or, for the purpose of study, with the eyes of the higher mammals. Even in such cases, though the eyes are generally paired and symmetrically placed, some instances of cyclopia (a congenital malformation consisting in the fusion of the two eyes into a single median one) are occasionally observed, but such cases are abnormal monstrosities, the study of which belongs to the branch of science termed Teratology.

A curious fact observed in the lowest class of amphibians represented by the triton and the salamander, is that of the regeneration of the ocular globe. Bonnet (1779) was the first to find that if the eyeball of a triton is partially destroyed it becomes reformed provided that about one quarter of the globe remains in the neighbourhood of the optic nerve. After an interval of time varying from one to six months, a small eye fitted with a transparent cornea and lens, with a normal iris and a new retina, is formed. This globe grows very slowly, and takes from twelve to fifteen months to reach the size of the other eye. The various parts are regenerated at the expense of what is left of the similar tissues; the cornea is formed from the sclerotic, the iris and ciliary body from the choroid; the retina grows at the expense of the pigmented epithelium and of the optic

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nerve trunk. The lens is formed by the proliferation of the cells of the superior pupillary edge of the iris.

This regeneration of the lens, which has been carefully investigated by Colucci, Bracher, Benoit and others, is of a nature to impress upon us the fact that the lens and the retina, apparently so different, present a similarity of origin easy to understand when we remember that these two structures are both ectodermic formations and can therefore grow on the same ground. During the few days following the extraction of the lens of a salamander or of a triton, the two pigmented layers which constitute the ciliary and iridic parts of the retina become the seat of a reaction characterised by a thickening and a depigmentation of these membranes. The phenomenon soon becomes localised at the upper pupillary edge; at this point the two layers, completely depigmented, swell so as to form a kind of vesicle, which increases in size by proliferation of its cells and by their transformation into crystalline fibres. When the regeneration is completed, the new lens severs its connection with the upper pupillary border and remains in contact with the iris, thus taking the place of the original lens.

There is no relation between the size of an animal and the volume of its eyes. For instance, among feline animals, the wild cat has eyes relatively bigger than those of the lion. The eyes of a whale are extremely small by comparison with the enormous bulk of the body. The elephant and the rhinoceros have eyes smaller than those of the horse, the antero-posterior length of which is about 41 mms. The eyes of the horse and the ostrich are the largest amongst terrestrial animals.

Some kinds of animals have very voluminous eyes compared to the size of the body. This is especially the case for birds. The eye of the owl represents a third of the volume of the head; that of the swallow represents 1-30th of the total weight of the body. On the other hand, amphibians and snakes have very small eyes; the eye of the common grass snake, weighing two centigrammes only (about a third of a grain) represents but one-thousandth part of the body weight.

Fishes living in a scantily illuminated medium have large eyes; the eye of a full-grown cod is as large as that of the horse, the eye of the shark is bigger still; the eye of Orthagoriscus reaches the size of a large orange, and its crystalline lens is about as voluminous as the human eyeball.

On the other hand, the eel and some other fishes burrowing in mud have small eyes and, as can be expected from the

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law of adaptation of any organ to surrounding circumstances, the visual organ may be arrested in its development in those animals to which an eye would be useless, i.e., in those animals living in complete darkness.

The eyes of bats, though not large, are usually fairly well developed, yet in some species they are so minute and so feebly organised that they impart the appearance of blindness; hence the popular expression "blind as a bat." In the long-eared bat the eyes are so small as to be hardly discernible, but they are more conspicuous in other species, e.g., the mouse-coloured bat. The eyes of most bats differ from those of other nocturnal animals in the fact that they are extremely diminutive, particularly in the parti-coloured bat and the Barbestella. In those types the eyes are at the bases of the ears, and often escape observation, as they are veiled by a long mouse-coloured fur.

The imperfect vision of bats is counter-balanced by the exquisite delicacy of sensation of the membranous wings, which serve to direct the animal in its nocturnal flights. Spallanzani has found by experiments that bats whose eyes have been entirely obliterated can fly through small apertures with the same precision as those with normal eyes.

The common mole has also very minute and imperfectly developed eyes, appearing as shining black globules lying deep in the skull, and often invisible owing to the soft velvety fur which covers them. This state of the eyes is adapted to the habits of the animal and to its mining and burrowing operations.

According to Ree and to Darwin, the eye of the mole is an instance of an organ which is rudimentary not by retention of fœtal character (i.e., by arrest of development) but by disuse aided perhaps by natural selection. This theory of atrophy by disuse which is observed in many other animals living in subterranean caves, is borne out by the fact that in all Cheiroptera of nocturnal habits, like the bat, the retina is fairly well developed with long rods and a very apparent visual purple.

From these brief considerations, it is possible to draw a general conclusion. Big eyes, giving large retinal images, are found in animals which move quickly and require a good, instantaneous vision; such is the case for birds, especially those of the nocturnal variety and, amongst mammals, for carnivorous animals.

In man and the higher monkeys, the eye is almost spherical in shape, hence the name of ocular globe. The human eye measures as an average, almost one inch (24.5 mms.) in its transversal diameter, a little less (roughly

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24 mms.) in its antero-posterior diameter, and still less (23.5 mms.) vertically. It weighs about 7 grammes, and has a volume of 6.5 cubic cms.

This spheroidal shape which is observed in the higher types of animals is, however, gradually departed from, and in a great many mammals the antero-posterior diameter is appreciably shorter than the other two principal diameters, but it is especially in fishes that this reduction is more marked. In many fishes the eye assumes the shape of an ellipsoid with three unequal axes; for instance, the three principal diameters of the eye of the pike, namely, the antero-posterior, the transversal and the vertical are respectively 10, 14 and 12 mms.; in the eye of the shark they are 40, 66 and 58 mms.

In the study of variations in the form of the eyeball, we must regard the bulb as made of three distinct portions, which may present important differences in shape. These portions are the corneal portion, the fundus portion, and the portion of the ocular wall connecting the two precedent ones; this third portion is termed the intercalar portion; it extends from about the anterior limit of the retina to the sclero-corneal junction. In man, monkeys and many herbivorous mammals, the intercalar portion is reduced to a very small extent, is slightly flattened, and the general shape of the eyeball remains approximately spheroidal. The intercalar portion, however, takes a great importance in the eyes of birds.

In the eagle-owl, the corneal portion is attached to the fundus portion by a kind of funnel with its outside surface concave; the internal surface of the funnel serves for the insertion of the ciliary muscle; the fundus portion of the bulb, in the form of a capsule of shallow depth but large curvature, is lined by the choroid and the retina. The proportion of the three portions forming the ocular bulb of the eagle-owl is as follows: 10.5 mms. for the corneal part, 17.5 for the intercalar or funnel-shaped portion, and 11 mms. for the fundus portion, giving a total antero-posterior length of 39 mms. The diameter of the posterior aperture of the funnel is 41 mms., whereas that of the anterior aperture is but 25 mms. It is probable that this peculiar disposition is intended to permit the formation of as large retinal images as possible for a minimum volume of the visual organ.

The intercalar portion is far from having the same importance in all birds; it is considerably reduced in the ostrich and in all aquatic birds, but its junction with the fundus portion always occurs under a sharp angle projecting forwards.

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In many fishes the intercalar portion almost disappears and the ocular capsule seems to be closed by an almost flat cornea. In fishes living in deep waters the bulb assumes, however, a peculiar shape, the intercalar part becomes considerably lengthened in the antero-posterior direction, and the eye assumes a form resembling that of a telescope; moreover, the two eyes are very near each other, and their axes are directed forwards in almost parallel directions.

This disposition, which would seem favourable to binocular vision is, however, an exceptional one in fishes; it has been observed in some species the eyes of which offer another peculiarity worth mentioning; the bulb is practically immovable in its orbit; the iris and the accommodative apparatus are completely absent, and the portion of each retina corresponding to the more anterior part of the eye, which is generally poor in sensitive elements, is differentiated into an accessory well-formed retina, probably intended to receive images of objects placed in the lateral parts of the visual field.

It has been suggested that the great difference in the appearance of the eyes of birds of prey, with their projecting and highly curved cornea, and that of the eyes of fish, with a cornea which was thought to be almost flat, was due to a special adaptation of the organ to the medium in which the animals live. This explanation is not wholly satisfactory, especially when we consider that, according to recent researches made by means of an ophthalmometer, it is proved that the cornea of fishes is not flat, at least not in the central portion, where it generally has a radius of curvature varying from 4 to 9 mms., which corresponds to a curvature about equal to or even greater than that of the human cornea.

It is more probable that the reason of the difference in appearance is this: the skull of a fish is attached to the vertebral column in an absolutely immovable way, and the eyes absolutely fixed in their orbits cannot be rotated; it follows that in order to see about him the animal has to move his body in different directions. The bird, on the other hand, has a fairly long and flexible neck, owing to which each eye can be turned in any direction. In fact, if we compare the eye to a photographic camera, we can say that the eye of a fish is a small camera with a wide-angle objective, giving small images but having a large field. In the bird, on the other hand, the camera has a long extension and the lens a long focus, so that the images are large but the field is comparatively narrow. This would explain why the eye of a fish is fitted with an almost spherical lens, the equatorial plane of which almost corresponds to the anterior

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limit of the retina, whereas in birds' eyes the equatorial plane of the lens is separated from the anterior limit of the retina by the whole length of the intercalar portion of the ocular wall.

**The Coats and Refracting Media of the Eye.**

It is hardly necessary to remind the reader of the fact that from the point of view of its anatomical structure the human eye is more perfect than that of any other animal, and that it consists of three superimposed coats and three refracting media.

From the periphery (or from the outside inwards) the coats are arranged in the following order. (See stereograms III. and IV. and descriptive line-drawings of each stereogram in appendix pages 407, 408, figs. 40 and 41.)

(1.) An outer membrane or sclero-corneal coat which forms to a certain extent the external skeleton of the globe.

(2.) A vasculo-muscular membrane, the uvea or uveal tract which is divided into three portions, the posterior one being called the choroid, the intermediate one the ciliary body, and the anterior one the iris.

(3.) A nervous membrane, the retina.

The three refractive media are, from the front backwards, the aqueous fluid, the crystalline lens and the vitreous body.

The whole globe is supported by a quantity of fat and loose connective tissue in the forepart of the orbital cavity somewhat nearer the outer and lower walls of the cavity than to the inner and upper walls. The four recti muscles and the two oblique muscles closely surround the greater part of the globe, and enable it to rotate within certain limits about a practically fixed rotation centre.

The lids are in contact with the covering of conjunctiva in front, and behind the globe receives the thick stem of the optic nerve which, as we shall see later on, expands so as to form the retina.

The human globe may be regarded as being composed of two segments of two separate spheres, of which the anterior (the cornea) is smaller and more projecting than the larger posterior sphere corresponding to the sclerotical part of the outer coat. The junction of the two is marked by a shallow groove termed the sulcus scleræ. The corneal sphere has a radius of curvature averaging about 7.8 mms., and forms but the anterior sixth of the whole eyeball, while the remaining 5-6ths are formed by the sclerotic, that is, by another segment of sphere the radius of curvature of which averages 12 to 13 mms. Fig. 19 shows the outline of the

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globe so constituted, the dotted lines indicating the portion of each of the component spheres which does not take part in the formation of the ocular globe.

It must be understood, however, that this is a purely diagrammatic representation of the human globe. As we shall see later on, the corneal portion of the outer coat is not strictly spherical, nor is it a portion of an ellipsoid of revolution. The most recent researches have shown that the cornea is not strictly of a uniform geometrical shape, and consists mainly of two parts, the central one (corresponding to the pupillar area) which is fairly spherical, at least in eyes free from corneal astigmatism, surrounded by a peripheral region which does not take any part in vision, and

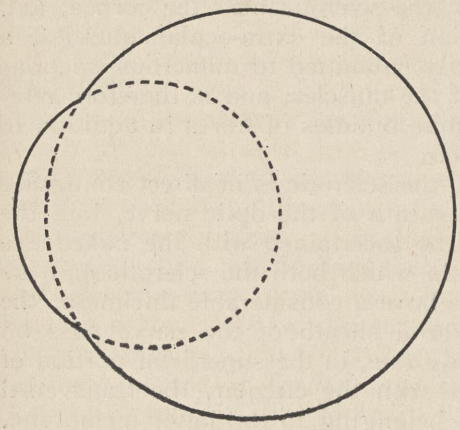

FIG. 19.

FIG. 19 shows diagrammatically the spheroidal shape of the average human eye. The portions of the diagram drawn in dotted lines indicate the parts of the two constituting spheres which do not enter into the formation of the globe.

is of a distinctly flatter form than the central or visual cap. We shall revert to the point presently. For the moment, and for the purpose of optical reasoning, we can regard the globe as having the shape indicated by Fig. 19.

A study of the coats and media of the eye will now occupy our attention.

**The Sclero-Corneal Coat. The Sclerotic.**

As already pointed out, the sclerotic and cornea, taken together, form the outer coat or what we might call the external skeleton of the eyeball.

The shape of the sclerotic corresponds to the general shape of the eyeball, since this structure forms 5-6ths of the whole external envelope. For the purpose of description we can regard the sclerotic as a portion of a sphere averaging 12 to 13 mms. in diameter, and as presenting two openings, one in front, one behind. The posterior opening gives passage to the optic nerve, as we shall see later on. It is not freely open, but forms a kind of sieve (the lamina cribrosa)

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through the holes of which the bundles of nervous fibres constituting the optic nerve enter the globe. The anterior opening corresponds to the cornea.

The sclerotic has, in its anterior part, a thickness of about 1 mm., i.e., is a little thicker than the rest of the coat, and furnishes a solid place of insertion to the recti muscles and to the ciliary muscle which are attached, the former at a distance of 6 to 7 mms. from the sclero-corneal junction on the outside surface, the latter to the internal surface of the sclerotic.

The sclerotic is mostly made of bundles of connective tissue fibres, some of which are directed longitudinally, some others transversally. This arrangement is especially marked in the portion of the sclerotic near the cornea, i.e., in the region of insertion of the extra-ocular muscles, a region which is necessarily submitted to numerous tractions due to the contraction of the muscles, and is therefore reinforced by numerous oblique bundles of fibres in addition to the two sets stated above.

In its posterior part, the sclerotic is in direct continuity with the outside fibrous sheath of the optic nerve, i.e., the dural sheath. This can be ascertained with the naked eye in the eye of the whale, in which both the sclerotic and the dural sheath of the nerve have a considerable thickness; the fibrous bundles of the dural sheath of the nerve pass on into the sclerotic or, at any rate, in the superficial portion of the sclerotic, and mingle with the circular, the transversal and the oblique bundles belonging to the latter membrane. In those animals the orbital cavity of which forms an insufficient protection to the eye, the sclerotic is very thick, especially in the posterior part; such is the case in many mammals whose orbit is open on the external side. In man, and most monkeys, the orbit forms a complete protective belt, and the sclerotic is reduced to a comparatively thin envelope.

In mammals and in man, the structure of the sclerotic is purely fibrous, but in all other vertebrates with an incomplete orbit its constitution is modified by the adjunction of cartilaginous and bony plates, the purpose of which is to secure a better protection for the eyeball.

Thus, in bony fishes, a cartilage, in the form of a half sphere with a hole for the passage of the optic nerve, extends as far in front as the ora serrata, and occasionally up to the corneal margin. The thickness of the cartilage is usually uniform, though, exceptionally, it is greater at the posterior part, as in sea tortoises, or again, at the anterior part, as in the shark

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In many fishes bony plates are superimposed on the cartilage on the nasal and temporal sides of the sclerotic. The structure of these plates is laminated and resembles that of dentine. These plates may take a considerable development, and ultimately join together to form a complete bony capsule surrounding the greater part of the eyeball.

In birds, we find two new bony formations of unequal importance. The first is a small ring-shaped or horseshoe-shaped bone surrounding the optic nerve entrance; it is termed the posterior sclerotical ring. The second, much more important, is the anterior sclerotical ring, which forms the skeleton of the intercalar portion of the ocular envelope. It is funnel-shaped and made of 12 to 15 scales overlapping each other.

**The Cornea**

which fits in the anterior opening of the sclerotic, presents, at least in its central area, i.e., the area corresponding to the pupil, a well-marked curvature, especially in the higher terrestrial animals and in man, in whom the radius of curvature averages 7.8 mms. It is this membrane, together with the aqueous fluid, which plays the most important part in the total refraction work of the eye. As we have already pointed out, the normal human cornea was thought at first to be spherical, but up to the time when Javal and Schiotz created a clinical method of ophthalmometry there was little known of the real form of the cornea. The original Helmholtz ophthalmometer being too complicated for clinical purposes, the measurements of the cornea obtained by means of this instrument were taken at three points of each meridian, namely, the point corresponding to the visual line and two other points on either side of this line. As the peripheral radii of curvature were found to be greater than the radius corresponding to the visual line, the idea that the cornea of the non-astigmatic eye was spherical had to be abandoned, and it was assumed that the corneal surface was in the shape of an ellipsoid of revolution about the long axis, which is directed outwards from the visual line and forms an angle (angle alpha) of about 5° with this line. This notion, however, differs widely from the reality; the cornea does not resemble an ellipsoid and Helmholtz was one of the first to point out the fallacy of this comparison.

After the construction of modern ophthalmometers or keratometers, it became much easier to study the question of the real shape of the cornea. The second model of Javal's ophthalmometer was fitted with a very large keratoscopic

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disc similar to a large Placido disc divided into graduations of 5° by concentric rings. After having made the usual measurements with the subject looking at the centre of the disc, the measurement was repeated by making him look 5° to the left, then 10° to the left, etc., and after having then measured the right half of the horizontal meridian, the left half was measured in the same way. We shall revert to the use of the Placido disc for a study of the shape of the cornea in the chapter devoted to the examination of the eye.

A similar measurement was made of the two halves of the vertical meridian. Without going into details which are fully dealt with in Tscherning's "Physiologic Optics," we shall simply say that such measurements were taken by Sulzer and Eriksen in Paris, and that they fully confirmed the views of Aubert and Matthiessen, who had used Helmholtz' ophthalmometer and had arrived at the conclusion that the cornea could be divided into two parts termed central and basilar respectively. The central one is approxi-

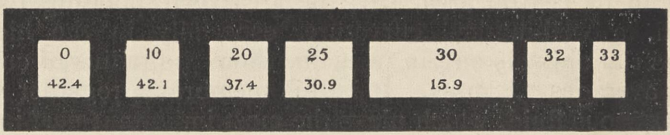


FIG. 20.

FIG. 20 (after Tscherning). Shape of the various zones of the cornea indicated by the appearance of the catoptric images of a well-illuminated square of white paper on a black background.

mately spherical in eyes free from astigmatism and of toric shape in astigmatic eyes; this part, which corresponds to the pupillary area, is called the optical or visual part. The surrounding or basilar part is much more flattened, less regular and less polished than the central portion. This basilar part does not intervene in vision unless the pupil is widely dilated, and the fact that it is less regular and less polished than the central or optical part explains the slight success of optical iridectomies.

Eriksen has tried to give a good idea of the variations of the radius of curvature of the cornea at various distances from the central portion by observing the shape which the corneal catoptric images of a square of a white piece of paper assumes when this paper is successively placed straight in front of the subject, and then, at angular distances of 10°, 20°, 25°, 30°, 32°, and 33° from the visual line in its normal position. Fig. 20, reproduced from Tscherning's book, shows the different forms corresponding to the internal half of the horizontal meridian. The number at the top of each square indicates the distance in degrees from the visual line, that

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at the bottom the corresponding refracting power in dioptres of the system formed by the cornea and aqueous fluid. We shall see presently that though the ophthalmometric measurement of the peripheral portion of the cornea takes too much time to be of service in clinical work, yet we can derive useful information in the matter by the means of the keratoscopic disc or Placido disc.

Since the optic system formed by the cornea and the aqueous fluid plays the greater part in the production of the total dioptric power of the eye, and since the power of the corneal system depends obviously on the curvature of the cornea, or at any rate, of the portion of the cornea corresponding to the pupil, it is clear that the optical importance of the corneal curvature diminishes in fishes and generally in aquatic animals, the eyes of which are immersed in a medium (water) the refractive index of which is not appreciably different from that of the ocular media, with the exception of the crystalline lens.

On the strength of Plateau's researches it had been thought for a long time that the cornea of a fish is practically flat and comparable to a plate of glass closing the ocular globe in front. This opinion has, however, been proved erroneous by ophthalmometric measurements of the central portion of the cornea of various fishes. These measurements show that the radius of curvature of the central area of the cornea of various fishes ranges from 2 or 3 mms. to 17 mms., according to the size of the whole eye. Plateau had tried to ascertain the corneal shape by means of casts, and his mistake is easily accounted for by the facility with which the membrane is depressed.

The shape of the sclerotical hole in which the cornea is fitted is generally that of an oval with the long axis horizontal even in spheroidal globes. The oval form of the cornea is well marked in the dog when the ratio of the horizontal and vertical meridians is that of 3 to 2. It is not so marked in other mammals and in man, in which it is almost circular though the horizontal diameter is slightly larger than the vertical one.

A curious feature of the cornea is shown in a species of fishes called Anableps (Anableps tetraophthalmos). The cornea is divided into two unequal portions by an opaque horizontal band. To each corneal portion corresponds a distinct pupillar aperture; thus we have two visual organs in a single eye, a kind of bifocal eye, one part of which is adapted for aerial vision when the fish swims on the surface of water, the other part for vision under water. Such bifocal eyes are not rare in Arthropoda (insects, etc.).



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The relative size of the cornea and of the whole globe varies widely. In turtles, in the chameleon, the whale, the corneal diameter, i.e., the diameter of the sclerotical hole in which the cornea is fitted, is to the diameter of the globe in the ratio of 1 to 4. In fish, the cornea is very large, the ratio being that of 1 to 1.3. In the mouse the cornea forms almost one-half of the sclero-corneal coat and the same condition is observed, though to a less extent, in the rat and the rabbit. Birds of diurnal habits have smaller corneæ, but in nocturnal birds the ratio approximates 1 to 1.8. In many mammals the ratio reaches the value of 1 to 2, i.e., the diameter of the sclerotical hole in which the cornea is inserted is about one-half of the diameter of the globe.

As a rule, large corneæ are found in animals living in comparatively dark media, like fishes, and in animals of nocturnal habits. In man, who has both diurnal and crepuscular vision the ratio of the corneal diameter to the antero-posterior diameter of the globe is that of 1 to 2.

**Microscopic Structure of the Cornea.**

Though we are mainly concerned with the gross anatomy of the eye, i.e., with the macroscopic (by contradistinction with the microscopic) investigation of the ocular coats and media, yet a brief account of the minute or histological structures of these parts is really necessary to obtain a clear understanding of the normal working of the eye.

Histologically, the cornea of man and of most vertebrate animals presents three main parts, namely:—

(1) An external layer, the epithelium.
(2) The substantia propria, or cornea proper.
(3) An internal layer lining the anterior chamber and termed the endothelium.

The external part is formed of two zones: the most superficial one is represented by an epithelium made of four or five strata of cells, and is continuous with the conjunctiva; the internal one, adjacent to the substantia propria, has been described as the anterior limiting membrane of the cornea, or as Bowman's membrane. Although it is still regarded by most anatomists as a separate formation, it does not materially differ in structure from the rest of the true corneal substance, and, moreover, it is absent in many vertebrates in which the substantia propria extends, without appreciable modifications, up to the external epithelium; such is the case in the rabbit and the guinea-pig.

The cells of the epithelium are arranged in three strata. The superficial one is made of flat cells; the intermediate one of polygonal cells; and the deepest one of cells with a

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flat base and a rounded apex; at the base of these cells processes are attached which penetrate in the subjacent layer. It is from the cells of the last-named stratum that the rest of the epithelial structure is formed.

Bowman's membrane, as we have already pointed out, has a variable thickness in vertebrate animals; it reaches its most complete development in fishes of the family of the sturgeon and the skate. In man, it has a thickness of 8 to 10 $\mu$, and, as we have already pointed out, it is hardly distinguishable in the rabbit and the guinea-pig. Its structure is always homogeneous.

The substantia propria forms the greater part of the cornea. It is made of tissue yielding gelatine on boiling and chemically similar to cartilage. All the constituents of this tissue, and of the whole cornea for that matter, have the same refractive index, so that in the perfectly fresh condition it is impossible, even with the best microscope, to make out any indication of structure. We shall come again on this point presently. After death, however, and with the assistance of reagents, the true corneal substance is found to consist of superimposed lamellæ made of connective fibres arranged in parallel bundles. These elements are united to one another by an amorphous cement, the name of which is derived from the parts it serves to connect (interfibrillar, interfascicular and interlamellar cement).

In most fishes the corneal plates are regularly parallel, and are traversed in a direction perpendicular to their surface by cylindrical fibres extending without interruption through the whole of the substantia propria. These fibres, known as the sutural fibres of Ranvier, are found in most vertebrates and in man, though to a variable degree; they always proceed from Bowman's membrane, but they do not reach as far as the posterior limit of the substantia propria. At the same time, the arrangement of the corneal plates becomes more intricate in the higher vertebrates; instead of being parallel, they are disposed in a more or less irregular way, with, between them, spaces or lacunæ which form a system of anastomosed canals filled with lymph, in which connective cells termed corneal cells or fixed cells, are immersed. These cells have ramified processes, which, by anastomosing with one another, form a reticulum connecting the cells themselves.

Beside the fixed corneal cells we have just mentioned, the substantia propria contains, in the intervals between the plates, a variable number of migrating cells, the movements of which are observable in the living cornea.

The internal portion of the cornea is formed of an elastic membrane, termed the posterior limiting membrane, or

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Descemet's membrane, lined by an epithelial layer made of irregularly hexagonal cells and termed the corneal endothelium, or the epithelium of the anterior chamber.

In man, and most mammals, Descemet's membrane is a strong elastic homogeneous layer, presenting, in transversal sections, bright and highly refracting striations. It is very resisting; when ulceration has destroyed the anterior layers of the cornea, Descemet's membrane may, for a considerable time, alone prevent rupture, but when finally it does yield, or when it is perforated in injuries of the cornea, it behaves like all elastic structures, the margins of the opening retracting and becoming curled on themselves.

The thickness of Descemet's membrane is not generally great, except in the horse, in which case it forms about one-eighth of the total corneal thickness. The endothelium is formed of a delicate but close mosaic of epithelial cells, flat in lower vertebrates, cylindrical or polygonal in mammals and in man.

At the periphery of the cornea, Descemet's membrane becomes a little thicker to form the tendinous ring of Dollinger. From this ring fibrils proceed, which are reflected onto the iris to form what is termed the reticulum of the iridic angle or the pectinate ligament, well developed in the ox, the cat, the pig, the rabbit, as well as in the human embryo; in man, in the adult state, it is not so well marked. In fishes, this reticulum is replaced by a solid mass which fills the iridic angle, and even covers a part of the surface of the iris.

**Nerve Supply and Nutrition of the Cornea.**

The cornea which, as we shall see later on, forms, together with the aqueous fluid, the main refracting apparatus of the eye, must evidently be transparent, or its essential purpose would be defeated. Most living tissues are nourished by blood-vessels, but, for the reason just stated, the cornea is an exception to this rule; blood-vessels would diminish the transparency of the membrane, and none of the corneal layers is vascular, at least in adult mammals. The spaces we have described in the true corneal substance form a network of anastomosed canals, in which lymph circulates and nourishes the cornea in a manner we will examine in another part of this work. (Chapter XVII.)

The cornea, on the other hand, is richly supplied with nerves, which proceed from a branch of the trigeminal or 5th pair of cranial nerves, the ophthalmic branch or ophthalmic nerve of Willis. Before they penetrate in the

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cornea these nerves lose their sheath of myeline, and subsequently their neurilemma which would render them more or less opaque and become reduced to their transparent cylinder-axes.

The corneal nerves are divided into two groups, the anterior and the posterior groups. The first forms, under Bowman's membrane, a plexus, the sub-basal plexus. From this plexus bundles of fibrillæ or divisions of axis-cylinders of very small thickness run straight outwards to the epithelium, piercing Bowman's membrane, and for this reason are called rami perforantes. On reaching the base of the lowermost tier of epithelial cells, each ramus breaks up into a pencil of delicate fibrils, which take a direction at right angles to that of the ramus itself, and, converging towards the centre of the cornea, form between the upper surface of Bowman's membrane and the base of the lowermost layer of epithelial cells, a close-set horizontal plexus of delicate fibrils, the sub-epithelial plexus. From this sub-epithelial plexus still more delicate fibrils run upwards into the epithelial layers, forming between the cells an intra-epithelial plexus, and from this extremely fine fibrillæ pass on upwards towards the outside surface. It has been asserted that these terminal fibrillæ project beyond the outside corneal surface, the free ends, swollen in tiny knobs, waving freely in the fluid which always bathes the cornea. This, however, has not been confirmed, but, in any case, the nerves of the cornea send off branches which end in free fibrils quite close to the surface, a fact which explains the exquisite sensibility of this part of the eye. It is hardly necessary to point out that the detection of the fine free endings of the corneal nerves requires special preparation; they are seen best with the gold chloride method of staining.

The posterior group of corneal nerves innervates the deep portions of the membrane, including Descemet's layer.

The complete study of the subject of the optical properties of the cornea does not come within the scope of this work. As we have already pointed out, the cornea, taken together with the aqueous fluid (i.e., what we might call for the sake of brevity, the corneal optic system) is the most important part of the dioptric apparatus of the eye, at any rate in man and in all higher animals living in air, owing to its two essential characters, namely, its regular shape (at least, in the portion corresponding to the pupil) and its perfect transparency. Strictly speaking, the cornea with an anterior surface of radius of curvature averaging 7.8 mms. and a posterior surface the radius of which is slightly shorter than 6.5 mms. really constitutes a concave meniscus,

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since it necessarily has its edges thicker than the centre. As, however, the corneal substance has a refractive index practically equivalent to that of the aqueous fluid, the posterior surface, thus immersed in a uniform medium (corneal substance in front of it and aqueous fluid behind), has no appreciable optical effect, and for this reason we can regard the cornea and aqueous fluid as forming an optical system, separated from air by a surface (the anterior corneal surface) the radius of curvature of which is averaging 7.8 mms. On that assumption the dioptric power of the corneal system is about 43D. It is the difference between the length of the radius of curvature of the anterior and that of posterior surface which explains the fact that the thickness of the cornea is slightly greater at the periphery than at the centre. A direct measurement of the corneal thickness is somewhat difficult on eyes removed from the body and prepared for sections, as the membrane becomes swollen by immersion in all liquids, especially water. After fixation in Müller's fluid (see Chapter XIX.) the cornea is permeated, especially in the posterior layer, and it is for this reason that on a section the posterior surface appears somewhat undulated and often shows a projecting swelling at the level of the edge of Descemet's membrane. Fixation by formol or alcohol is the best to secure the appearance of normal anatomical conditions.

As we have already remarked, the convex form of the cornea is not a general feature in the eyes of all living beings. Considerable variations are observed in various animal species. In aquatic mammals and in fishes, the cornea is relatively less curved than in the human eye, but this is counteracted by the fact that the lens is much more convex; in fact, the lens of many fishes is practically a sphere. Man seems to have the smallest cornea by comparison with the size of the eye. In the rabbit and in nocturnal mammals and birds it reaches a considerable size.

In the case of some diseases or anomalies of the eye, the human cornea and the globe may assume an enormous size, as is shown in buphthalmos. On the other hand, and owing to an arrest in the embryological development of the eye, the whole globe and the cornea may be of a size considerably below the normal (microphthalmia).

The cornea occupies, as we know, the anterior portion of the globe and is partly covered by the lids; the upper lid covers about one-sixth of the corneal area, while the lower lid is practically level with the inferior margin of the cornea. It is only in the portion corresponding to the palpebral aperture and especially in the central and paracentral part

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of the cornea, i.e., the portion corresponding to the pupil, that this membrane is practically spherical, at least in eyes free from astigmatism. This region corresponds to what is called the optical zone, and even in this region, the corneal curvature is usually slightly greater in the vertical than in the horizontal meridian, thus giving rise to the low degree of corneal astigmatism which is the almost general rule in the normal eye.

**Transparency of the Cornea and of the Ocular Media generally.**

The transparency and the perfect polish of the corneal surface, at least in the optical zone is, of course, a physiological necessity. To explain the transparency of the cornea we cannot do better than to give a quotation from Prof. Ranvier :—

"Here is a block of glass, quite transparent. Let us break it up and hammer the fragments until the whole block is transformed into a mass of very fine particles, which we collect into a test tube. This mass, though made of transparent glass particles, separated from each other by air, which is also transparent, is perfectly opaque. If we pour water on it we give it a certain degree of transparency, but to restore to the mass its original transparency we have to fill the interstices between the glass particles with Canada balsam, whose refractive index is practically that of glass." The explanation of this experiment lies in the fact that a body is transparent when all its elements, however different in structure, are all of the same optical density, i.e., of same refractive index.

This condition is fulfilled in the cornea; not only the cells of the epithelium, the anterior basal membrane, the plates and cells of the substantia propria, Descemet's membrane and the cells of the endothelium have the same refractive index, but the various parts constituting each of these elements, for instance, the bodies of the cells, their nuclei, the sutural fibres and the intercellular cement also have the same refractive index. The proof of this is found in the impossibility to distinguish these elements from each other when examined under the microscope in the living state. The same applies to the aqueous fluid, the vitreous and the crystalline lens.

Of course, the aqueous and the vitreous have not exactly the same index as the cornea, and in this respect the latter differs appreciably from the lens; we even find a difference in the index of the nucleus and that of the cortical portion of the crystalline lens, but these differences, which

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co-operate to the focussing of luminous rays, and to the formation of retinal images, do not affect the transparency of each part considered separately.

Thus, the condition for the transparency of a tissue depends on the uniform index of the various elements constituting this tissue. A further proof of this is afforded by the circumstances in which the transparency of the ocular media may accidentally disappear.

A transient opacity of the cornea occurs after death. The fact, observed long ago by Louis, a French military surgeon of the time of Napoleon the First, has been carefully investigated by Ranvier and du Bourget. They found that in man, about 12 hours after death, a corneal opacity appeared simultaneously in the two eyes, in the form of concentric rings, which fuse together and finally vanish without leaving any trace. The explanation given by Ranvier is that the fixed cells acquire a refractive index higher than that of the surrounding medium; this is shown by a microscopic examination of a cornea in which the opacity has just begun to appear; the cells are distinctly seen, and their nuclei, at first invisible within the cells, become more and more apparent.

The cornea is rendered opaque by aqueous imbibition of the fibres constituting the substantia propria. Such an opacity may be produced by scratching the posterior or endothelial surface which is in contact with the aqueous fluid; in this case again the cells become visible under the microscope, because they do not absorb water and their index remains higher than that of the fibres forming the plates, since the latter have become less refracting owing to their swelling. In the case of ordinary connective tissue, maceration in water is sufficient to exhibit the fibrillar structure; for instance, a fragment of tendon appears after maceration as a bundle of isolated fibrils. In the case of the cornea, however, it is only possible in this way to obtain a very uncertain striation, and a complete dissociation is impossible. As Ranvier puts it, the corneal fibres swell in the same manner as dried up gelatine.

Mechanical compression and extension also render the cornea opaque. The fact is well known to oculists who have learnt to recognise in this form of opacity a sign of extreme tension of the contents of the eyeball in the affection termed glaucoma.

The same result may be obtained artificially by compression of the whole globe, or by direct compression of the cornea between two glass slides, or again by a traction in opposite directions on the two extremities of the membrane.

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The degree of opacity is proportional to the intensity of the force exerted, and, on relaxing the pressure or the traction, the corneal tissue regains its transparency. A microscopical examination gives the key to the phenomenon; a striation is seen, which denotes a change of refracting power of the fibres, while the liquid medium escapes the effect of the compression or traction.

The cornea becomes opaque by freezing, and its transparency is restored by thawing. A similar phenomenon is observed in the crystalline lens and the conclusion is evidently that, in both structures, some parts, richer in water, are more strongly affected by the change in refracting power which accompanies freezing. At the temperature of ebullition of water, the cornea and the lens are again rendered opaque; the effect of the heat is to alter to a variable degree the index of the fibres, the cells and their nuclei, and thus to render these elements distinct from each other.

Strong electric discharges also determine the opacification of the cornea, the cells are killed, and their ruptured nuclei acquire a new index, owing to which they are distinguishable from the rest of the corneal tissue. In the same circumstances, the crystalline lens becomes opaque, i.e., cataracted. Some instances are recorded in the case of men struck by lightning.

**The Sclero-Corneal Limbus or Sclero-Corneal Junction.**

Our description of the sclero-corneal coat would not be complete if we were not giving a few supplementary details on an important part of it.

The sclero-corneal limbus forms the limit between the sclerotic and the cornea. It is somewhat difficult to observe it on stained sections, but it is located about 1 mm. from the imaginary line joining the peripheral ends of Descemet's and Bowman's membranes, this line being always easily seen with a moderate magnification. The limbus is thus a small region formed by the anterior limit of the sclerotic, which is bevel cut at the expense of the internal portion, and encroaches over a similar corneal bevel cut at the expense of the external surface. The encroachment of the sclerotical bevel over the corneal one is more marked at the upper than at the lower portion of the limbus, and this explains why, as we have already pointed out, the cornea does not appear exactly circular, but has a horizontal diameter slightly greater than the vertical diameter.

The limbus is interesting from the physiological point of view, since it is at this level that the excretion of the aqueous fluid takes place, as we shall see later on. It is interesting

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also from the surgical point of view, since it is the seat of the incision performed in many operations on the globe.

In fact, the tissue of the corneal limbus is a zone of transition between the corneal tissue proper and the sclerotic. It is somewhat less transparent than the cornea though more transparent than the sclerotic; it shows some blood-vessels and numerous nervous fibrils; besides, it contains a vascular canal which we shall describe presently as Schlemm's canal.

In topographic order, it would be necessary to describe now the anterior chamber, its contents (the aqueous fluid) and the circulation of the latter. This portion of our subject will, however, be better understood at a later stage.

**The Cornea as a Part of the Refracting or Dioptric Apparatus of the Eye.**

As we have mentioned before, the cornea (and aqueous fluid) form the most important part of the refracting apparatus of the eye. The corneal system has a dioptric power of 43D, i.e., about $2\frac{1}{2}$ times that of the lens *in situ*. In the average normal eye, the slight difference between the curvature of the vertical and that of the horizontal meridian causes a slight direct astigmatism which does not usually exceed 0.5 or 0.75D. This is compensated in most eyes by a corresponding degree of inverse astigmatism due to a slight inclination of the crystalline lens with respect to the visual axis of the eye. It follows that the so-called physiological corneal astigmatism is not noticed by the subject nor is it detected by subjective testing or with the retinoscope, though it is shown by a careful ophthalmometric measurement.

Hence the reason for the empirical rule that the correcting cylinder prescribed for actual wear should not be exactly that indicated by the ophthalmometer and that the difference between the subjective astigmatism and the keratometric astigmatism is obtained by an addition of 0.5 or 0.75 D against the rule to the value given by the ophthalmometer or keratometer. This rule is obviously a merely empirical one. Javal had been able to establish a relation between the two values, and the results obtained from his formula agree fairly accurately with observed facts.

It must be understood, however, that the physiological direct astigmatism is more exactly compensated by the inverse astigmatism due to inclination of the crystalline lens when the subject is young. In fact, this compensation is not entirely due to obliquity of the crystalline lens, but to a slight extent to irregular contraction of the ciliary muscle. This has been proved by Terrien, who has observed a case of contusion of the globe which, together with a spasm of

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accommodation, had determined a fairly high degree of temporary astigmatism. This disappeared after a few days at the same time as the ciliary spasm.

As we shall see later on, the hardening or sclerosis of the lens may also be the cause of a variable degree of astigmatism. The fact has to be borne in mind in the correction of the refraction in subjects of comparatively advanced age. This astigmatism of lenticular origin is chiefly characterised by the variation in the orientation of the principal meridians. Up to about 40 the vertical meridian has a slightly higher power than the horizontal one, which gives rise to the so-called physiologic astigmatism unless the defect is exactly compensated by an inverse lenticular astigmatism. The correcting cylinder, if convex, has then its axis vertical. The direction of the axis alters with advancing age, and tends to become inclined sometimes on the nasal, sometimes on the temporal side. Hence the necessity in the case of elderly subjects to verify the power, and still more so the orientation of the axes of the cylinders every 2 or 3 years.

The cause of these variations lies partly in the cornea, partly in the lens. The sclerosis of the latter and the irregular contraction of the ciliary muscle seem to have a predominating effect, but there is no doubt that the corneal curvature is also modified. The fact, which is easily verified by means of the keratometer, is probably due to loss of the tone of the palpebral muscles. A partial closure of the lids or a prolonged pressure on the globe brings an increase in the power of the vertical corneal meridian. In fact, the physiologic corneal astigmatism is most probably due to the pressure exerted on the vertical meridian of the globe by the constant effect of the orbicularis muscle. A similar effect is obtained by a prolonged pressure on the globe in the direction of its vertical diameter.

This is proved by careful ophthalmometric measurements of the horizontal meridian of the cornea, the only accessible meridian when the lids are partly closed; such measurement compared with the measurement of the same meridian when the eye is open shows clearly that the curvature of the horizontal meridian during partial closure of the lids is diminished, this diminution being obtained at the expense of a proportional increase of curvature in the meridian (the vertical) which is submitted to a pressure. Many cases are recorded of astigmatic subjects whose astigmatism is more or less completely eliminated by a pressure exerted on a particular part of the globe; a careful examination shows that the meridian corresponding to the

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point of pressure is the meridian of minimum power, and it is obvious that the effect of the pressure is to equalise more or less completely the curvature of this meridian and that of the meridian at 90° to the first.

The decrease of the muscular tone and the slight eversion of the lower lid margin which accompanies it in elderly people is calculated to have the opposite effect.

**The Sclero-Corneal Coat as an Organ of Protection.**

Together with the sclerotic the cornea forms the external skeleton of the eye. The cornea itself is protected by its anterior epithelium which, like all covering epithelia, may be reformed when partly destroyed at the expense of the deeper portions which constitute the true regenerative layers. This purpose of protection is purely mechanical, and the anterior corneal epithelium simply acts as a shield and its functions are not comparable to those of the bulbar conjunctival membrane; owing to its mobility and elasticity, the conjunctiva slides easily on the subjacent tissue and on the capsule of Tenon. It is mainly the conjunctiva which defends the globe against infection, and therefore plays a most important part in the protection of the cornea.

This protective effect of the conjunctiva and corneal epithelium is clearly shown by the study of the healing of corneal wounds.

In such cases, the healing process consists of two different phases: the first (termed the epidermic phase) takes place at once, the second or dermic phase occurs a little later. For instance, in a case of corneal ulcer, the loss of substance is immediately made good by a production of new epithelium or more exactly by a mechanical phenomenon which is easily observed if very small and superficial wounds are made in the cornea of a rabbit by means of a razor. The epithelial cells of the edge of the wound appear to roll into the cavity artificially created in the same way as marbles contained in a bag would escape if the bag is opened at any point. This is the epidermic phase of reparation. When this is completed, the fixed cells of the portion of stroma which corresponds to the wound emit processes which anastomose with each other and form a lattice-work which pushes forward the epithelium and ultimately replaces it. The tissue thus regenerated is of a less transparent character than the normal corneal tissue, and constitutes the scar or relative opacity which is so often the sequel of corneal ulceration.

If the corneal epithelium only is involved in the wound or scar, the process of repair takes place without leaving any trace, and the cornea conserves its transparency, but if the

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stroma (substantia propria) is involved, a scar or nebula will be the consequence, the density of the relative opacity being in proportion to the amount of stroma which has been destroyed.

The subject of the nutrition of the cornea is of importance. Though the cornea is not supplied with blood-vessels, it is the seat of phenomena of nutrition, some of which are purely physical (exosmosis and endosmosis); some others are of biological nature, and consist in phenomena of absorption and diffusion. The medium of nutrition is the lymph characterised by the presence of white blood corpuscles or leucocytes which, though not abundant in the normal state, serve by their migration to produce the exchanges constituting the corneal metabolism.

In cases of inflammation their number increases considerably, and they may give rise to infiltration as occurs in the interstitial keratitis.

Beside the leucocytes, we have mentioned the existence of fixed cells in the cornea, and these cells (or keratoblasts) are, as we have seen, the main agent of the dermic phase of reparation.

Blood-vessels, completely absent from the normal cornea, may show on the surface in cases of pannus or in the thickness of the membrane when there is a considerable infiltration as is the case in interstitial keratitis. In such cases they help the resorption of the leucocytes and stimulate the process of reparation. A fuller account of the nutrition of the cornea will be given at a later stage—together with a brief description of the clinical examination of the sclero-corneal coat.

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# CHAPTER IX.

## THE UVEAL TRACT. THE CHOROID.

**The Uveal Tract Generally.**

If we remove carefully the sclerotic and cornea—i.e., the outside coat—from the eyeball of a mammal, we get a spherical mass, coloured in dark brown by the pigment it contains. On account of the similarity of this dark sphere, hanging upon the optic nerve as upon a stem, to a grape, the middle tunic of the eye has been called by ancient anatomists the uvea or uveal tract (from uvea, a grape). This denomination is not strictly correct since it includes in the uveal tract the pigmented layer forming the outermost retinal layer. As we have seen in the chapter devoted to the embryological development of the eye, the pigment layer of the retina, though it generally sticks to the choroid when an attempt is made to separate the two structures, really belongs to the retina and is derived from the proximal part of the primary optic vesicle in which the distal part becomes invaginated to form the secondary optic vesicle. We are thus able to understand that in the embryological development of the eye, the mesodermic envelope of the secondary optic vesicle is at first a single one; at a later stage of development the layer near the retina, that which contains the nutrition blood-vessels of the latter membrane, becomes separated, by cleavage, from the more external layer which forms the sclero-corneal coat. In the anterior portion of the globe, this cleavage gives rise to the formation of the anterior chamber, while in the intermediate and posterior portion, it gives rise to the suprachoroidal space, to which we shall revert presently.

The zone where the primitive envelope remains unseparated from the subjacent parts serves to the passage of the anterior ciliary vessels and to the attachment of the uveal tract. The portion of the tract in front of this zone constitutes the iris. In lower vertebrate animals, fishes, for instance, the rest of the tract constitutes the choroid. It is only with the apparition of the accommodative apparatus that the third or intermediate portion of the uveal tract as we know it in man and in the higher mammals becomes differentiated and forms the ciliary body.

In birds, the part of the sclerotic which corresponds to the ciliary body is the part we have already alluded to under the name of intercalar zone. This zone is very reduced in

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size in the human eye, and the ciliary body corresponds to the sclero-corneal junction and to the portion of sclerotic slightly behind it and included between the sclero-corneal junction and the ora serrata.

The whole of the internal surface of the uveal tract has a double lining. Over the hind part, behind the ora serrata, the choroid is lined by the single layer of hexagonal pigmented cells forming the pigment epithelium, and by the retina itself. In front of the ora, in the portion corresponding to the ciliary body, the uvea is lined by the same layer of pigment representing the outer lamina of the retinal cup or secondary optic vesicle, and by a layer of cells, more or less free from pigment, representing the inner wall of the cup and called the pars ciliaris retinæ. As the uvea extends forwards to form the iris, these two layers continue with it and line the back surface of the ocular diaphragm up to the pupillary margin, which thus marks the extreme lip of the secondary optic vesicle.

We shall describe separately the three portions of the uveal tract, namely, the choroid, the ciliary body and the iris, and study the function of each of these parts.

**The Choroid.**

The choroid represents a segment of a hollow sphere placed between the sclerotic and the retina. Its thickness is generally small and comparable to that of the cerebral pia mater or the arachnoid sheath of the optic nerve, of which it is but a prolongation. Even in the larger types of animals, the choroidal thickness is little above half a millimeter, though it reaches one and even one and a half millimetres in the sea lion and the whale.

The minute structure of the choroid is frequently a subject of difficulty to the student, owing to the apparently different descriptions given in various text-books; some authors describe three layers, some others five or six; these differences are merely a matter of classification, as we are going to show.

**Microscopic Structure of the Choroid.**

In man, the choroid is formed of the following parts, from without inwards:—

(a) The suprachoroid, separating the choroid from the sclerotic;

(b) The choroid proper;

(c) The lamina vitrea which separates the choroid from the retina.

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If we observe the choroid *in situ* after the globe has been opened and the vitreous and the retina removed, the inner surface appears smooth and uniformly brown. Then, if we try to peel it off from the sclerotic, we notice that at several spots it is more firmly attached than at others; the most intimate connection occurs at the margin of the aperture for the optic nerve, and also in the places where the vessels and nerves enter the choroid from the sclerotic, especially in the region of the posterior pole (point of penetration of the posterior ciliary arteries) and at the equator (region of exit of the venæ vorticosæ). When, after having torn away these connections and separated the choroid from the sclerotic, we get a view of the outer surface of the former membrane, we see it has a shaggy appearance because of the shreds of tissue adhering to it.

Thus, we find that the choroid proper is separated from the sclerotic by a loose areolar connective tissue, non-vascular but more or less pigmented and made of fibres extending from one membrane to the other. On separating the two structures, part of this tissue clings to the sclerotic and part to the choroid, the latter part giving the membrane the shaggy appearance we have just mentioned. Some anatomists regard the part of the tissue adherent to the sclerotic as constituting the lamina fusca, while they call suprachoroidal membrane, the part remaining with the choroid. Some go even further and consider the part of the suprachoroid which clings to the sclerotic as being sclerotical in nature, the other part being choroidal; this division is not justified; an examination of an ox's or a sheep's eye shows clearly that the whole of the suprachoroid is truly a choroidal structure.

The choroid proper consists of three main parts, namely, the layer of large vessels, the layer of medium-sized vessels, and the layer of capillary vessels or choriocapillaris.

The layer of large vessels, or Haller's layer, is made of the trunks of the ciliary arteries, short and long, with the branches into which they break up on the one hand, and on the other hand, the ciliary veins gathered up from the ciliary body and iris as well as the choroid itself; the vessels anastomose freely and form a dense network. Haller's layer is comparatively thick, occupying about three-quarters of the entire choroidal thickness. The spaces between the vessels are filled with pigment cells or chromatophores, forming a dark background to the vessels which, on a surface view, appear as bright lines on this dark ground. It is the pigment of this layer which constitutes the dark background

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to the orange-coloured vessels in the ophthalmoscopic examination. Numerous elastic elements occur in the layer of large vessels.

The layer of medium-sized vessels is very thin and but moderately pigmented; some anatomists do not regard it as a different structure from the previous one.

The layer of capillary vessels, or Ruysch's layer, consists almost completely of capillaries of a large bore which anastomose freely in all directions and are so closely packed that the spaces between them are often smaller than the vessels themselves. Pigment cells never appear in the choriocapillaris layer in normal conditions.

The lamina vitrea, or Bruch's membrane, is a thin, highly transparent and structureless membrane covering the inner surface of the choroid proper, and on which rests the hexagonal pigment epithelium, the outermost retinal layer.

The hexagonal pigment layer was thought by older anatomists to be a part of the choroid, but as we have shown in a previous part of this work, it is now known to be formed by the outer or distal portion of the primary optic vesicle invaginated within the proximal portion; it therefore really belongs to the retina though, on attempting to separate this membrane from the choroid, the pigment epithelium generally remains with the choroid. Pathologically, however, the pigment epithelium may well be regarded as forming a part of the choroid; thus, what is usually termed a detachment of the retina is really a separation occurring between the pigment epithelium which remains applied to the choroid and the rest of the retinal layers.

**The Part Played by the Choroid and the Retina in the appearance of the Ophthalmoscopic Picture of the Fundus.**

The colour and brilliancy of the ophthalmoscopic picture of the fundus is modified by the relative amount of pigment contained in the retinal epithelium or hexagonal pigment epithelium on one hand, and in the chromatophores or pigment cells of the choroid on the other hand. Usually, the amount of pigment in the epithelial layer of the retina corresponds to that in the choroid, but disproportionate pigmentation of the two membranes is not uncommon. As a rule, the fundus of a blonde individual is light in colour, that of a brunette dark, but there are exceptions. The following normal variations in fundus pigmentation produce the more familiar types of eye-ground:—

(a) Excessive pigmentation of both choroid and retinal epithelium, as in negroes, produce a poorly illuminated



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fundus, slate coloured at the posterior pole, chocolate colour at the periphery.

(b) A moderate amount of pigment in the retinal epithelium may be sufficient to hide the choroidal vessels and still permit the passage of a brilliant reflex from the choroid; in such cases, the fundus has a uniform, rich red colour.

(c) If the retinal epithelium is well pigmented and the choroid rather poor in pigment, the epithelium becomes visible and the fundus appears stippled or "peppered."

(d) If the retinal epithelium is poor in pigment, the choroid can be seen through it. In such cases, if the pigment is abundant in the intervascular spaces of the choroid, a tesselated or tigered fundus is produced and the choroidal vessels appear of a lighter colour than the background.

(e) If both the epithelium and the choroid are poor in pigment, the choroidal vessels are darker than the background and the fundus appears reticulated.

(f) In albinism and in cases of fundus depigmentation the choroidal vessels are distinctly seen, sharply defined against a yellowish-white sclerotic.

**The Tapetum Lucidum.**

The name of tapetum has been given to a reflecting layer interposed between the choriocapillaris and the layer of medium-sized vessels in the choroid of many vertebrates. Cartilaginous fishes like the skate, the sturgeon, and the shark, and many teleostens or bony fishes present a tapetum. This structure is absent from the choroid of amphibians and of most birds, but exists in a great many mammals, especially cetacea, carnivora, ruminating animals and most of the higher ungulates (horse, elephant).

In cetacea (whales) and fishes, the tapetum covers the whole fundus, but in most other animals it is limited to that portion above and outside the entrance of the optic nerve which seems to be the seat of monocular and perhaps binocular vision. When a tapetum exists the retina is deprived of pigment on the corresponding area.

In fishes, the tapetum must not be confused with the argentine membrane, a special tunic of a brilliant silvery white which occurs between the suprachoroid and the layer of large vessels of the choroid proper. The suprachoroid, which covers the outside surface of the argentine tunic or argentine membrane, being poor in pigment in fishes, the latter membrane appears immediately the sclerotic is cut open. The argentine tunic contains a considerable number of small

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crystals of guanine which give it its characteristic appearance; it is hard and extends forwards up to the pupillary border of the iris. Its thickness is even greater in the portion corresponding to the iris than in the portion corresponding to the choroid, and as, in the former portion, it is only covered by a small quantity of pigment cells, it gives the iris of a fish its peculiar brilliant appearance. It must be observed that since the internal surface of the argentine tunic is lined by the heavily pigmented layer of large vessels, this tunic cannot play the part of a reflector as is the case for a true tapetum.

The tapetum of fishes has a structure resembling that of the argentine tunic; its metallic appearance is due to crystals of guanine enclosed within the body of large cells disposed between the choriocapillaris and the layer of medium-sized vessels. In mammals the tapetum does not contain crystals of organic substance like that of fishes, and its brilliancy is much less marked. It occurs in two distinct varieties differing by their anatomical structure.

In carnivorous animals and in the sea lion, the tapetum consists of cells smaller than those containing the crystals of guanine in fish; these cells assume the form of thin plates in which phenomena of interference occur. The cellular elements of the tapetum are in immediate contact with the choriocapillaris layer; in the cat and dog, there are five or six cellular strata and, in places, ten to fifteen, the thickness of which varies from 20 to 40 microns. The thickness of the cells is very small and their outline is hexagonal or irregular; the cellular contents are granular and of a yellowish tint when examined by transmitted light.

The tapetum of carnivorous animals has a metallic reflex, yellow or greenish, varying to light blue or to steel-blue towards the periphery. The most visible portion, clearly circumscribed, has the form of a crescent. The tapetum begins immediately above or inside the papilla or even on it; the whole of its surface forms a scalene right-angled triangle with three processes or branches, the hypotenuse passing through the papilla. Owing to its anatomical structure, the tapetum of carnivora is termed a cellular tapetum by contradistinction to the fibrous variety found in almost all ruminating animals.

The general arrangement of the fibrous tapetum is very much the same as that of the cellular tapetum except that the interferential cells are replaced by flat bundles of fibrillated lamellæ; these bundles have an oblique direction with respect to the subjacent choroidal vessels; the fibres are undulated and extremely fine. Fairly thick at the centre, where it

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presents a green reflex, the layer constituting the tapetum becomes progressively thinner towards the periphery and assumes a bluish tint.

Beside the difference in their structure, the cellular and the fibrous tapetum differ in another way. If the eye of a carnivorous animal is enucleated and opened, the colour of the tapetum fades rapidly in daylight, and if the pigment of the retinal epithelium, lying immediately below the lamina vitrea, is removed with a camel-hair brush, the colour likewise vanishes, even in the dark, the choroid then resembling a piece of dirty wash-leather. In the case of the fibrous tapetum, brushing away the retinal pigment has no effect on the colour, which remains and keeps its tint in daylight, and even in a weak solution of formalin.

The tapetum may easily be detached from the layer of medium-sized choroidal vessels; it is more difficult, but possible, to separate it from the choriocapillaris layer.

In some birds, the ostrich for instance, there is a choroidal layer of lamellar structure, reflecting light with production of interferential colours, but the phenomenon can only be observed after the retinal pigment epithelium, the pigmentation of which is very heavy, has been removed; strictly speaking, this is not a true tapetum.

The existence of the tapetum accounts for the variously coloured glares shown in the eye of carnivorous or ruminating animals when viewed in comparative darkness. The phenomenon is, of course, well known, but the glare was for a long time attributed to a spontaneous production of light in the eye, to a photogenic function of the retina, a kind of phosphorescence like that of the glow-worm; it was supposed that anger or surexcitation of the animal increased the intensity of the glare.

It was Prevost of Geneva who, in 1810, proved in an irrefutable manner that the glare cannot be seen in an absolutely dark room, that neither the animal's will, nor any stimulation brought to bear on it, could bring about a production of light and that the phenomenon was always due to a reflection of incident rays by some part of the fundus acting as a mirror. The results of the anatomical researches we have resumed just now entirely agree with Prevost's views; the relative positions of the observed eye, the source of light and the observer's eye for which the glare is of greatest intensity shows that the latter is produced by reflection at the tapetum. The fact that the glare persists for some time after the death of the animal is a further confirmation of Prevost's theory and shows that the retina has no photogenic power.

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The colouring of the light reflected by the tapetum is not one of pigment, but of iridescence, like the colouring of Newton's rings and thin films; it is due to the interference of light in the special layer we have described; in herbivorous animals, interference is brought about by the peculiar arrangement of fine bundles of fibrillated connective tissue; in carnivorous animals, by the minute crystals contained in the cells of the tapetum.

The purpose of the tapetum is not well elucidated. Some physiologists think that rays of light which have traversed the retina a first time are reflected back along the axes of the rods or cones in an opposite direction, thus allowing a more perfect utilisation of light and enabling an animal with a tapetum to perceive dimly illuminated objects better than an animal having no such structure. There is very little doubt that the existence of a tapetum is generally associated with a higher light-sense—i.e., with perception of low degrees of illumination—but the above theory is open to objections; there are many nocturnal or rather crepuscular animals without a tapetum, for instance, the owl, the mouse, and many of the inferior monkeys.

The existence in the human eye of a formation corresponding to the tapetum of ruminating or carnivorous animals has been the subject of many discussions. The human pupil generally looks black and does not show the glare observed in some animals. This appearance was explained by Haller, Boerrhave and most of the physiologists at the end of the 18th and the beginning of the 19th centuries, on the assumption that the deep membranes of the eye completely absorbed the light entering through the pupil; if such were the case, any attempt to see the fundus of a living eye was doomed to failure.

It was well known, of course, that the pupils of many carnivorous and herbivorous animals could, under certain circumstances, appear luminous, but as we have stated before, this was explained by a spontaneous development of light under the influence of the nervous system. Yet, as far back as the beginning of the 18th century, Mery had found that on immersing an animal's head under water, not only could he see the pupil luminous, but he could even distinguish what he called the choroidal vessels, in reality the retinal vessels. His experiments were made to support the views of Mariotte, who regarded the choroid as the immediate organ of vision; since he could see the interior of the eye, he had come to the logical conclusion that the deep membranes did not absorb the light entering the pupil.

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Later on, the mathematician de la Hire attributed the fact to the change in refraction caused by the immersion of the eye, and thus recognised the real nature of the phenomenon; he gave the path of the incident rays and that of the rays reflected by the deep membranes of the eye in the case of the eye in air and in the case of the immersed eye. But such was the authority of Boerrhave and Haller that their theory was regarded as one of the dogmas of physiologic optics. Even Prevost's conclusions did not receive the attention they deserved, and it was only when Helmholtz published his work on the theory of the ophthalmoscope (1851) that the doctrine of the absorption of light by the deep membranes of the eye was definitely abandoned.

Sattler has demonstrated the existence, in the human eye, of an intervascular layer formed of fine elastic fibres arranged in laminæ, somewhat in the same way as those constituting the tapetum of herbivorous animals; yet, the human eye does not show anything resembling the reflex observed in the eye of animals with a tapetum.

**Survey of the Structure of the Choroid.**

To sum up, the choroid in man and in the higher vertebrates consists of the three main following parts:—

(1) An external part, the suprachoroidal membrane separating the sclerotic from the choroid proper. Some anatomists regard it as made of two separate structures, namely, the lamina fusca and the suprachoroidal layer. Its thickness varies in different individuals and in different species: in man, it is more developed in dark eyes than in blue eyes. To separate it easily from the subjacent parts, hardening in Müller's fluid is the best method. The suprachoroid is made of superimposed lamellæ, each of which is constituted by a reticulum of fine elastic fibres with pigmented cells.

(2) A vascular portion, called the choroid proper, made almost entirely of blood-vessels with branched pigment cells. The choroid proper is subdivided into three layers, the layer of large vessels, the layer of medium-sized vessels and the layer of capillary vessels or choriocapillaris layer. Pigment cells are abundant in the layer of large vessels, in moderate quantity in the layer of medium-sized vessels, and absent from the choriocapillaris layer. In carnivorous and ruminating animals as well as in many herbivorous ones, and in cartilaginous fishes, a special layer, the tapetum, is inserted in the layer of medium-sized vessels or between this layer and the choriocapillaris; this special layer is reduced to a vestigial remnant in the human eye.

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(3) A basal membrane, the lamina vitrea or Bruch's membrane, which separates the choroid from the retina, and on which the retinal pigment epithelium rests.

The choroid of birds, amphibians, and reptiles is built very much in the same way. In the class of bony fishes or teleostens, the blood-vessels of the choroid form, round the point of entrance of the optic nerve, a projecting mass called the choroidal gland by ancient anatomists who misinterpreted its nature. It is not a gland at all, although the name has remained, but a cluster or a plexus of vessels, some arterial, some venous. The choroidal gland is very well marked in the eye of the pike, where it appears as a thick mass, located in the region of the entrance of the optic nerve between the argentine membrane and the vascular portion of the choroid; it may be regarded as a local hypertrophy of the vascular part of the choroid. Cuvier thought that the choroidal gland was an erectile organ serving to displace the plane of the retina, and thus to adapt the eye to different distances. We know now that this opinion is erroneous, and that the choroidal gland plays no part whatever in accommodation.

**Physiological Functions of the Choroid.**

The choroid is often described as forming the camera obscura of the eye, and for a long time, the opinion of Kepler that the choroidal pigment simply served the same purpose as the black varnish coating the internal surface of optical instruments was generally adopted by physiologists. It is known now that the choroid is not so much a light-absorbing membrane as a reflecting one. A careful examination of the choroid will show that the reflecting power is greater than the absorbing power; the latter could only have an appreciable value if the surface were rough, but such is not the case; the choroid is smooth and fairly well polished in the portion corresponding to the retina. It is merely in the portion corresponding to the internal surface of the ciliary body and iris that the uveal membrane presents the rough appearance which is required from a light-absorbing surface; anywhere else, the choroid acts as a mirror reflecting rays of light onto the outermost layer of the retina, the layer of rods and cones. In inferior animals we have seen that the retinal rods are oriented towards the incident light; they receive, therefore, their luminous stimulation on the extremity corresponding to that of the sensitive elements of the human retina which is immersed in the pigment epithelium.

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The analogy between the eye and Lipmann's method of colour photography is striking; Lipmann obtained negatives in natural colours by placing a reflecting mirror, made of a mercury trough, behind and in direct contact with the sensitive film of the plate, thus reflecting the light which had passed through the translucent film onto the particles of silver haloid, the colour effect being obtained by interference. In the eye, light passes through the transparent retina which may be compared to the sensitive photographic film, and is reflected back by the choroid to the ends of the rods and cones which are analogous to the particles of silver bromide or chloride of the photographic plate. We may well ask ourselves with Dr. Lindsay Johnson: "Do we not owe our colour sense to interference also?"

We have no positive evidence of any kind in favour of this theory, but at the same time, no purely physical theory of colour vision has been brought forward which will meet all objections.

The choroid serves other useful purposes. It is well known that any nervous apparatus must be maintained at a certain degree of temperature in order that it may perform its functions. Many facts of observation as well as numerous surgical applications show that anæsthesia occurs as soon as a nervous fibre is sufficiently cooled at some point on its path or at its extremity. It follows that a sensitive apparatus must be accompanied by some apparatus supplying the necessary heat. The retina is no exception to this rule, and its nervous elements could not perform their function if the eye were not kept at a proper temperature. The calorific apparatus of the retina is the choroid which forms round it a kind of hot chamber owing to its abundant vascularisation and its rich circulation.

Finally, the choroid plays an important part in the nutrition of the retina and in maintaining the shape of the eyeball. The eye is, broadly speaking, a shell filled with fluid and semi-fluid contents. For the various functions of the eye, it is necessary that this shell shall be filled to a certain extent, not more and not less, and this fulness, this "intraocular tension" which corresponds to about 25 mms. of mercury, is provided by the lymphatic arrangements of the choroid.

If the retina were not adequately supported by the vitreous humour, if it could flap about or in any way alter its curvature, the dioptric arrangement of the eye would be upset; if the vitreous body at one time shrank, at another expanded, the movements of accommodation could not be

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carried on; if the aqueous fluid were now abundant, now scanty, the movements of the pupil would become irregular and uncertain; and if the whole globe were so flabby as to give way under the pull of each extra-ocular muscle, the delicate movements of the eyeball would become impossible. It is through the lymphatic vessels and the choroid that the eye is kept in the required condition of tension, but this aspect of the subject will be more readily understood when we study the nutrition of the globe as a whole. Just now we shall merely examine, in a very brief manner, the part played by the choroid in the nutrition of the retina.

The retina is, to a certain extent, nourished by the plasma of the blood exuding through the thin walls of the capillary vessels forming the choriocapillaris layer of the choroid. At least, it is so in retinæ entirely deprived of blood-vessels, as is the case in the horse, especially if there are no vessels in the vitreous or no other vascular arrangement capable of replacing the absent retinal vessels.

In the human retina, however, the innermost layers only are supplied with blood-vessels, as we shall see later on, and it is most probable that the rest of the membrane (hexagonal pigment layer, bacillary layer and outer nuclear and outer molecular layers) are nourished by the fluid oozing through the walls of the capillary vessels of the choroid. To quote Dr. Lindsay Johnson, all secreting layers and glands consist essentially of three parts. First, a network of blood-vessels, usually followed by one of capillary vessels; secondly, a basement membrane; and finally, a layer of secreting cells. In the uvea, we find an abundant supply of blood-vessels arranged in three rows which, commencing from the outside of the choroid are: Haller's layer, consisting of large anastomosing vessels; the layer of medium-sized vessels intimately connected with the tapetum when this structure exists; the choriocapillaris layer which is in close contact with the outer surface of the basement membrane or lamina vitrea. Finally, in contact with the inner surface of the latter layer, we find a layer of densely pigmented secreting cells which constitute the hexagonal pigment layer of the retina throughout the whole extent of the choroid.

The choriocapillaris secretes the fluid necessary for supplying the laboratory of the hexagonal pigment layer, which latter seems to have a double function, viz., to nourish the external layers of the retina and also to secrete the visual purple which envelops the free ends of the rods and, as we shall see later on, serves to adapt the eye to low degrees of illumination. The subject of the nutrition of the retina is not completely elucidated, however.

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Direct experimentation seems to prove the fact stated above, namely, that the non-vascular parts of the retina derive their nourishment from the choriocapillaris. When fluorescein is injected into one of the ciliary arteries, the characteristic green coloration is soon observed in the outer retinal layers, but the flow of the colouring fluid seems to experience great difficulty in penetrating the rest of the nervous membrane. Yet, if the retina is detached from the choroid, it conserves, at least for some time, all its vital properties, and when reapplied, it may resume its physiological work, even after a somewhat prolonged period of separation. On the other hand, when deprived of its own circulation, as in cases of embolism of the central artery, the retina loses its sensibility to light. Beside, on the part corresponding to a spot of choroidal atrophy, or above a congenital coloboma of the choroid, the retina may have its full sensorial power in spite of the absence in these parts of the choriocapillaris layer, no doubt owing to its own blood-vessels. We shall revert to the subject when studying the nutrition of the eyeball generally.

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## CHAPTER X.

### THE UVEAL TRACT—*(Continued)*. THE IRIS AND THE CILIARY BODY.

**The Iris.**

The iris forms the anterior segment of the middle or vascular coat; it is the contractile and coloured membrane which is seen behind the transparent cornea and gives the eye its colour. Slightly towards the inner side of the centre of the iris is a circular opening termed the pupil.

At its circumferential border, which is nearly circular, the iris is continuous with the choroid or more exactly with the ciliary body, and by the pectinate ligament it is united to the cornea. The iris does not hang as a flat curtain behind the cornea, as its pupillary border rests on the anterior lens surface which is convex, while its circumferential attachment is slightly farther back than the pole of the lens; it follows that, in normal conditions, the iris is slightly bulging forwards. By lying in this way upon the lens, the iris obtains a firm support. Hence, if the lens is absent or has lost contact with the iris, the latter is seen to tremble with every movement of the eyeball (tremulousness of the iris or iridodonesis.) The iris measures about 11 mms. across, and its thickness, when the pupil has its average size of 3 to 5 mms., is about 0.5 mms. When the pupil is widely dilated, the thickness of the iris is practically doubled.

**The Microscopic Structure of the Iris.**

The stroma of the iris is chiefly made of blood-vessels running in a radial direction from the ciliary margin to the pupillary margin. These vessels are supported by a small amount of connective tissue, in which are more or less numerous pigment cells. The pigment contained in them is yellow or of lighter or darker shades of brown. The supporting connective tissue consists chiefly of cells and fibres, the latter being arranged in bundles directed for the most part radially towards the pupil. There are a number of communicating interfascicular spaces forming a system of lymph spaces within the stroma of the iris.

On its anterior surface, the stroma is covered by an epithelium continuous with the endothelium of the cornea, and consisting, like the latter, of a single layer of polygonal cells. On its posterior surface, the stroma is lined by a fibrillated membrane, the posterior limiting membrane of

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the iris or membrane of Henle. The fibres constituting this membrane are directed radially, and are regarded by most anatomists as being of muscular nature, i.e., as constituting a muscle, the dilator of the pupil, which is supposed to act antagonistically to the sphincter of the iris. Physiologically, there is no doubt that the posterior limiting membrane acts as a dilator of the pupil, but a theory has been recently advanced to the effect that the pupillary dilatation it produces is the result of elastic and not of muscular traction. We shall revert to the subject presently.

The posterior limiting membrane is in its turn lined by the two laminæ of the retina representing the two layers of the secondary optic vesicle, namely, the pigment epithelium layer and the more or less pigmented layer formed by the mere framework of the retina since the nervous elements of this membrane disappear from the ora serrata onwards. Hence, the posterior limiting membrane of the iris is covered on its posterior surface by a double pigmented layer which represents the continuation of the retina up to the pupillary margin. For this reason, this layer is often spoken of as the iridic part of the retina (pars iridica retinæ) in contradistinction to the other layers of the iris, which, taken together, constitute the uveal part of the iris.

The pigmented layer thus forming the innermost iridic layer not only extends to the pupil, as stated just now, but it often turns round the pupillary margin and appears on the front surface as a small black rim, easily seen when the eye is viewed from the front. The more contracted the pupil is the broader this becomes, and when the pupil is greatly dilated it may entirely disappear; this narrow dark fringe stands out with especial prominence in eyes affected with cataract, for it contrasts more forcibly with the whitish background of the clouded lens than with the black pupil of the normal eye.

The muscular involuntary or unstriped fibres constituting the sphincter of the iris are disposed circularly and concentrically around the pupil in the deeper part of the stroma. They form a narrow band varying from 0.5 mms. to 1 mm. in width, according to their state of contraction. The muscle does not extend quite to the pupillary edge, from which its inner margin is always separated by a small zone of the iridic tissue.

As we shall see presently, the nature of the dilating apparatus of the pupil is still in discussion. Recent researches made independently by Grynfelt and Vialleton have confirmed the existence of a true dilator muscle, and proved that this muscle is composed of the radial fibres of

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the anterior portion of Henle's membrane which, as stated previously, separates the iris stroma from the retinal pigment layers. According to these authors, the dilator of the iris would be formed by the anterior poles of the cells of the pigmented layers differentiated by radial striations. Each of the cells in Henle's membrane would be of muscular nature at its anterior pole and pigmented at the posterior pole. Such cells would thus belong to the category of the myo-epithelial cells similar to those found in the body of the fresh water hydra.

It follows that there is really in the human iris a dilator membrane of fibrillar structure instead of an ordinary muscle built on the usual plan. Embryological considerations confirm this assumption inasmuch as they show plainly that the dilator membrane (or Henle's membrane) is of ectodermic origin, and derives from the external layer of the embryo retina, that layer which forms the pigment epithelium and also the membrane of Bruch. This view, which was advanced by Vialleton, has been confirmed by Nusbaum, who recognised that not only Henle's membrane but also the sphincter muscle itself are of ectodermic nature, whereas most of the other muscles in any part of the body derive from the mesoderm.

The analogy between the two iris muscles, namely, the sphincter and the dilator, is therefore absolute, only in the sphincter the differentiation is more complete, and is not limited to the anterior poles of the cells as is the case for the dilator.

It should be clearly understood that the power of the dilator is very weak indeed, since the muscle is entirely contained in Henle's membrane, the thickness of which is only about two to five microns. It is most probable that the weak effect of the contraction of the dilator may be increased by the regulation of the calibre of the arteries contained in the iris stroma. This regulation, which occurs under the influence of the sympathetic nervous system, consists in relaxation and contraction of the thick muscular coats of the arteries. Indeed, it is a fact of observation that the pupillary size is not fixed for any length of time, but constantly oscillates within very narrow limits, and it can be ascertained that these slight rhythmical changes can be produced artificially in a corpse by alternately injecting and withdrawing fluid from the arteries. Furthermore, Munch is of opinion that the cells of the stroma itself are endowed with some sort of muscular power and thus help in the production of pupillary dilatation. He arrived at this conclusion by analogy with the nature of the cells of the choroidal

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stroma. The proofs advanced by Munch in support of his opinion in the case of the iris are numerous and varied. A particularly interesting one is that based upon the eversion of the pupillary margin in a movement of enlargement; the phenomenon is easily verified by an examination with the binocular loupe or the corneal microscope. Another proof is the fact of the rolling up observed when a fragment of the iris is cut off in an operation of iridectomy.

We have said that the anterior surface of the iris is covered by a thin epithelial layer which is really the continuation of the endothelium of the cornea. Depressions of some size, termed crypts or stomata, have been described in the anterior surface of the iris. They are really openings leading into the lymph spaces of the stroma, which are thus in free communication with the anterior chamber. This arrangement is favourable to the rapid changes which must occur in the volume of the iris when the pupil dilates or contracts.

Beside these crypts, the front surface of the iris shows waving lines and more or less intricate markings which mainly consist of projecting ridges formed by the blood-vessels of the stroma. As a rule, these markings are running, like the blood-vessels which cause their production, from the circumference of the iris to the pupillary margin. Near the latter, however, they interlace with a ring of circular ridges (the lesser circle of the iris or circulus minor iridis). This circle divides the iris into two zones; that lying outside the circulus minor is termed the ciliary zone, that lying within the circulus minor is much narrower and is termed the pupillary zone; the latter is often of a coloration different from that of the ciliary zone. In the normal eye, these markings are well defined and clear but, in an inflamed iris, they become effaced and indistinct owing to the exudation of lymph, thus affording an important sign of iridic disease.

During intra-uterine life the pupil is closed by a thin, semi-transparent vascular membrane the vessels of which are continued from those of the iris and of the capsule of the lens (which is also vascular at this stage of development). Near the middle of the pupil the vessels loop round leaving the centre free from vessels. They disappear two or three months before birth, becoming obliterated from the centre towards the periphery and the membrane itself is gradually absorbed in a like manner. As we have pointed out, a few shreds may remain at birth and sometimes the whole membrane persists.

The colour of the iris, which is either light (blue or grey) or dark (brown) is caused by the iridic pigment. There

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are two kinds of pigment in the iris, namely, that which lies in the branched pigment cells of the stroma and is therefore called the stroma pigment, and that which is contained in the iridic part of the retina (retinal pigment). Upon the proportion between the amount of pigment in the stroma and in the pars iridica retinæ, the coloration of the iris depends.

The retinal pigment is generally very abundant, whereas the amount of stroma pigment varies in individuals and at different periods of life. At birth the retinal pigment is fully developed whilst the stroma pigment is almost entirely absent, the stroma itself being thin and fairly translucent; hence the deep blue colour of the eye of a new-born child. This coloration is an effect of interference. Any black background viewed through a translucent medium appears blue. This is the explanation of the bluish tint of the superficial veins of the body; these vessels, filled with dark venous blood, are really almost black, yet they appear blue when seen through a moderate thickness of translucent skin.

If the stroma, though deficient in pigment, is fairly thick and compact, the iris appears grey and the greater the amount of brown stroma pigment, the more this pigment becomes visible and makes the eye appear brown, while the retinal pigment, which lies behind, is more and more concealed and withdrawn from view.

Not infrequently, in an iris that is lightly pigmented as a whole, one or two isolated accumulations of pigment are found in the stroma which stand out as dark or rust-coloured or brown spots in an iris otherwise grey or blue. The presence of a pretty large number of them gives the iris a mottled appearance. The pigmented spots referred to just now may resemble foreign bodies which, after having penetrated within the eye by a corneal wound, have become fixed upon the iris surface. By a curious play of nature the pigmented spots and the markings on the iris may arrange themselves in such a way that they constitute letters or numerals. Such an occurrence is rare, but there are on record a few well authenticated cases. The most extraordinary one is that of a woman on whose irides the number 45 in the right eye and the number 10 in the left were clearly marked. A remarkable case of the same kind can be seen in the Dupuytren Museum of the School of Medicine in Paris. It goes without saying that such freaks of nature have no real significance. Exceptional cases occur in which the iris has no pigment in the stroma though there is always some in the retinal epithelium; such eyes are said to be affected with albinism.

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**The Size of the Pupil. Pupillary Reactions.**

It should be clearly understood that there is no such thing as a normal size of the pupil. In healthy individuals the pupillary size may range from 1 or 2 to 6 or 7 mms. and, except in extreme cases, it is impossible to be certain that the size of the pupil is abnormal unless we know the average size of that particular person's pupil. In some cases it is difficult to get the pupil to contract below 3 mms., and in others this is the extreme limit of dilation. These differences in sizes depend on differences in the structure of the iris. As a rule, the pupil is large in children and in myopes, and small in elderly people and in hyperopes. In fact, it is noteworthy that a small pupil is met with at the extremes of life, i.e., in very early infancy and in advanced age.

We shall examine later on the mechanism of pupillary reactions. For the present it is sufficient to say that the iris performs two main functions; firstly, it controls the amount of light entering the eye (the less the illumination the larger the pupil, and conversely) thus preventing an intense light from injuring the retina. Secondly, it cuts off the marginal rays which would, unless arrested, diminish the sharpness of the retinal images owing to the spherical aberration of the optic system of the eye, i.e., to the difference in refracting power of the periphery of the cornea and lens from that of the centre.

Normally both pupils are of equal size, and any difference, unless present from birth, is due to some pathological condition.

The reaction of the pupil takes place involuntarily and unconsciously; it is either a reflex action in which case the stimulus is transmitted from the brain to the nerves supplying the sphincter or the dilator of the iris, as occurs in an increase of illumination, or it is associated with some other movement of the eye as, for instance, in the act of accommodation, when the pupillary fibres of the 3rd nerve are set into action simultaneously with those supplying the ciliary muscle.

The pupillary reflexes are three in number, namely, the light reflex, the reflex to associated movements (accommodation and convergence), and the reflex to sensory stimuli.

The light reflex is sub-divided into the direct and the indirect or consensual reflex. The former consists in the alteration which takes place in the size of the pupil when, one eye being occluded, the other is exposed to varying degrees of illumination. The direct light reflex is easily observed. The subject under examination is directed to cover

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one eye not merely with his hand, but by means of a handkerchief rolled into a ball so as to exclude all outside light. Light is then shaded from the eye under investigation by means of the hand or of a cardboard screen; when this is withdrawn, the sharp contraction of the pupil due to luminous stimulation is observed; on replacing the hand or the screen in front of the eye, i.e., on sheltering that eye from light, the pupil is seen to dilate. The same manœuvre is effected in regard to the other eye. Should the contraction of one pupil be more sluggish than that of the other we can infer that the light conducting power of that eye is lessened. We shall refer to this important point later on.

The indirect or consensual reflex of the pupil is the alteration that takes place in the pupil of the covered eye when the other eye is being tested for its response to direct light stimulation. In a state of health, the consensual reflex is equal to and synchronous with the direct reflex.

The pupillary reflex in associated movements always takes the form of a contraction of the pupil, and occurs (a) in convergence, when the sphincter of the iris acts in conjunction with the internal recti muscles; (b) in accommodation, when the sphincter acts in conjunction with the ciliary muscle.

The convergence reflex is best observed by directing the patient to look first into the distance and then at an object (a finger or a pencil) held within a few inches of the eyes. The contraction of the two pupils should be equal and synchronous, though not so well marked as the contraction due to light.

The reflex to accommodation is examined in each eye separately, and in the same way as the convergence reflex, or again it may be observed in the two eyes at the same time. It has been argued that in the latter case the reflex (or pupillary contraction) depends more on convergence than on accommodation, but this opinion is negatived by the fact that the pupillary contraction still occurs when one eye is occluded. On the other hand, and when both eyes are open, the contraction occurs even in fairly highly myopic subjects who must converge to see the near object viewed, but do not require any accommodation; this would prove that the reflex in associated movements is dependent more on convergence than on accommodation.

In a disease of the spine termed locomotor ataxia, the pupils do not react to light, but do so to accommodation and convergence. This condition is called Argyll Robertson's pupil.



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The reflex to sensory stimuli is observed in special circumstances. Tickling of the skin in various parts of the body and strong psychic emotions, such as fright, produce a dilatation of the pupil.

**Hippus.**

A condition of the pupil which is worth notice is that termed hippus. This is an exaggeration of the normal changes in the pupillary size which constantly occur in the healthy subject from every change in illumination, or in accommodation or in convergence. These changes are very slight in normal conditions, but it may happen that in a group of diseases which are a frequent stumbling block to the optician (namely, the toxic diseases of the retina and optic nerve, and especially retro-bulbar neuritis) the normal and very slight oscillations of the pupillary size are exaggerated, and this constitutes the condition called hippus. In this condition, one finds that the pupil reacts to light and to associated movements like a normal pupil though the contraction may be relatively slow; instead, however, of remaining contracted as a healthy pupil does, it oscillates and slowly expands again.

The nervous mechanism of the pupillary reactions and the application of these reactions to the localisation of interruptions on the path of visual impulses will be investigated in the part of this work devoted to the nervous apparatus of the eye.

**The Ciliary Body.**

Immediately continuing the iris posteriorly we find the ciliary body, which can be exposed to view by bisecting the eyeball and removing the lens and the vitreous, as is explained more fully in the chapter on Dissection. We know that the retina, the innermost coat of the eye, ends anteriorly in a jagged line termed the ora serrata, or, to be quite accurate, the retina ceases to contain nervous elements at the ora serrata and its continuation forwards consists merely of the pigment epithelium layer and another layer, more or less pigmented, which represents the inner lamina of the secondary optic vesicle, i.e., the retina proper deprived of nervous elements, and reduced, therefore, to the connective tissue constituting the supporting framework of the nervous part of the sensitive membrane of the eye. Corresponding to the ora serrata, there is a change in the colour and appearance of the inner surface of the uvea, which is brown and smooth behind this line, black and rough in front of it.

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**Ciliary Muscle.**

At the level of the ora serrata (see fig. 21) the choroid becomes considerably thickened owing to the existence of the ciliary muscle. The main part of the muscle arises by a thin, flat expansion from the sclero-corneal margin, its fibres being attached to the bundles of the pectinate ligament. The fibres forming the outermost portion of the muscle, that is, the portion nearer to the sclerotic, are directed meridionally backwards and inserted into the choroid about midway between the equator of the globe and the level of the ora serrata. This portion of the ciliary muscle is termed the tensor of the choroid or muscle of Brucke.

The inner portion of the ciliary muscle consists of circularly arranged fibres, appearing in cross section when the eye is cut longitudinally. It is generally called Müller's muscle, from the name of the anatomist who discovered it. The two portions of the ciliary muscle are not generally sharply defined and, in most eyes, there are intermediate or transitional fibres, the path of which passes gradually from the radial direction observed in Brucke's muscle to the circular or annular form, as is seen in Müller's muscle.

Müller's muscle thus forms a sphincter ring round the external margin or circumference of the lens; it is often called the circular ciliary muscle, and plays an important part in the act of accommodation. It is extremely developed in hyperopic eyes, is much less developed in emmetropia and low or moderate myopia; it may even be entirely atrophied in eyes affected with high myopia.

In the human eye, the fibres of the ciliary muscle are of the unstriped variety and, therefore, the muscle is comparatively slow to respond to nervous impulses. In birds, especially those flying at great speed, the ciliary muscle is of the striped variety and is quick acting, a character well adapted to the conditions of life of those animals.

The ciliary body is, as we have stated above, the continuation forward of the choroid, i.e., it is the portion of the uveal tract intermediate between the choroid and the iris.

On the whole of the posterior hemisphere of the globe and even on the more posterior portion of the anterior hemisphere, the choroid is directly applied on the sclerotic. As the choroid reaches a position about midway between the equator of the globe and the sclero-corneal junction, it slightly bends away from the sclerotic, leaving between this coat and itself a space, triangular in section, which is occupied by the ciliary muscle. From the point where the choroid separates from the sclerotic, the former structure becomes thicker and its innermost, deeply pigmented portion

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is thrown into a series of radiating folds, the ciliary processes, about 70 in number, which proceed towards the circumference of the lens and form round the periphery of its back surface a sort of indented collar. (See fig. 21 and stereograms V., VI. and XIII.)

FIG. 21. DIAGRAMMATIC MERIDIONAL SECTION THROUGH THE ANTERIOR PORTION OF THE EYE MAGNIFIED ABOUT 12 TIMES, SHOWING THE SCLERO-CORNEAL JUNCTION AND THE FILTRATION ANGLE. (Fuchs).

*S* is the sclerotic and *C* the cornea, the boundary between which shows a cross section of Schlemm's canal *s*. Anteriorly, the outer or sclero-corneal coat is covered by the limbus of the conjunctiva *D*. Farther back, a cross section of an anterior ciliary vein is seen in the sclerotic at *ci*. The root of the iris is attached to the sclero-corneal coat by the pectinate ligament *l*. As the pupil is somewhat contracted, the iris is long and thin and its pupillary border is drawn out into a thin edge. On the anterior surface of the iris some of the orifices of the crypts appear at *cr*, together with the contraction furrows *f f*. The posterior surface of the iris is lined with a double sheet of pigment (the iridic part of the retina) which turns sharply like a spur at the pupillary edge *p*. At one spot a portion of the posterior layer of this double pigmented lining is separated from the more anterior layer; this is due to an accident in the process of preparation, but this detail is useful to show that the iridic part of the retina is made of two separate layers, namely the anterior one which corresponds to the retina proper, deprived of its nervous elements and reduced from the ora serrata onwards, to a slightly pigmented layer, and the posterior one, consisting of the pigment epithelium layer.

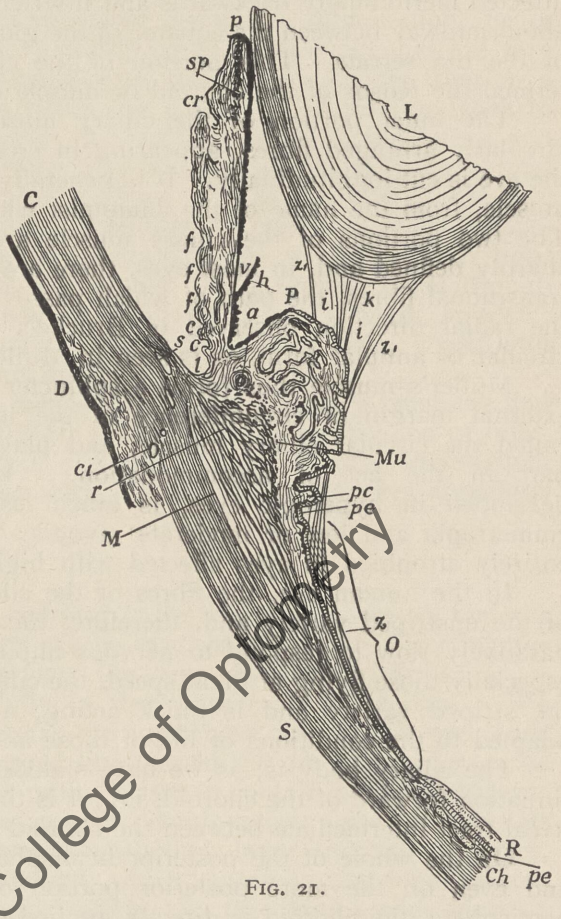


FIG. 21.

Close to the pupillary margin, the fibres *sp* of the sphincter of the iris are seen in cross section. From the sclero-corneal junction, close to the canal of Schlemm, the ciliary muscle arises, consisting of longitudinal or

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meridional fibres *M* and of circular fibres *Mu*; the former, which are inserted in the choroid, constituting the tensor of the choroid, the latter, the muscle of Müller. The transition from the longitudinal to the circular fibres of the ciliary muscle is effected by the radial fibres *r*.

At the anterior margin of the circular portion of the ciliary muscle, the cross section of the major arterial circle of the iris is seen at *a*.

Upon the ciliary muscle the ciliary processes *P* are situated; these are lined by the two layers of the ciliary part of the retina, namely the pigmented layer *pe* which is the continuation of the pigment epithelium of the retina and a less pigmented layer *pc* which is the continuation of the retina proper *R*, reduced from the ora serrata to a framework free from nervous elements. The flat part of the ciliary body, the orbiculus ciliaris *O* extends to the ora serrata, where the retina proper *R* and the choroid *Ch* begin. Upon the orbiculus lie the fibres of the zonule of Zinn *z*, which farther forward pass into the free portion $z^1$ of the zonule and enclose the canal of Petit *i*. The lens *L* shows at its equator, besides the attachment of the zonular fibres, the cross section *k* of the ring of nuclei of the cells forming the inner epithelium of the anterior lens capsule.

**The Ciliary Processes.**

The arrangement of the ciliary body is best studied in meridional sections; in such sections it appears triangular in shape with the base, or short side, looking forwards and giving rise, from about its middle point, to the iris. The inner side bears the ciliary processes, and the outer side corresponds to the ciliary muscle.

Thus we can regard the ciliary processes, i.e., the folded portion of the ciliary body, as being the direct continuation of the choroid, the portion of the uveal tract intermediate between the choroid and the iris; the muscular portion of the ciliary body (or ciliary muscle) is interposed in the space left between the sclerotic and the anterior part of the choroid. The structure of the ciliary processes is similar to that of the rest of the choroid except that the stroma, i.e., the portion corresponding to the choroid proper, does not contain any pigment towards the free extremities of the folds.

Exactly as in the case of the iris, the ciliary body is lined on its inner surface by the two layers representing the two laminæ of the secondary optic vesicle, namely, the pigment epithelium layer of the retina and the more or less pigmented layer consisting of the retina proper deprived of its nervous elements, which disappear at the level of the ora serrata. These two layers form the ciliary part of the retina and are continued at the posterior surface of the iris up to the pupillary margin under the name of iridic part of the retina.

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# CHAPTER XI.

## THE REFRACTING MEDIA OF THE EYE.

**The Anterior Chamber and the Aqueous Fluid.**

Our investigations of the anatomical structure of the eye and of the life of the visual organ will be somewhat simplified if, instead of proceeding at once to the study of the inner or nervous ocular coat, we proceed with the study of the refracting media, which, as we have already pointed out, are three in number, namely, the aqueous fluid, the crystalline lens and the vitreous body.

Owing to their similarity of origin, we will deal first with the aqueous humour and the vitreous body.

Between the iris, which is the extreme anterior part of the uveal tract, and the cornea, which forms the front part of the sclero-corneal coat, the very narrow lymphatic space we have described as existing between the sclerotic and the choroid becomes more conspicuous and forms a wide chamber termed the anterior chamber. This chamber, upon the establishment of the pupil by absorption of the embryological formation termed the pupillary membrane (see page 146), becomes continuous with the smaller posterior chamber, i.e., the almost virtual space between the back of the iris and the ciliary processes on the anterior side and the suspensory ligament and the front surface of the lens on the posterior side. (Fig. 21 and stereogram XII. show the posterior chamber.)

The cavity of the conjoint anterior and posterior chambers constituting together the aqueous fluid chamber is really a continuation and an enlargement of the flatter and much smaller space between the sclerotic (which, as we shall see more fully presently, may be regarded as the continuation of the dural sheath of the optic nerve) and the choroid, which is but the continuation of the middle sheath of the nerve. The aqueous chamber may thus be likened to the spaces between the sheaths of the optic nerve which are themselves a continuation of the spaces between the sheaths of the brain.

The anterior and posterior chambers, like the lymphatic spaces of which they are but an extension, contain a peculiar fluid, the aqueous fluid or aqueous humour; this is a clear, colourless liquid, alkaline in reaction, of a specific gravity of about 1.005, and is chiefly made of water with but 0.86 per cent. of solid matter, mostly mineral salts, and 0.05 per cent. of proteid or albumin together with 0.05 per cent. of sugar.

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The refractive index of the aqueous fluid is generally given as being the same as that of pure water, namely, 1.333 or 4/3 and regarded as equal to that of the corneal substance, though the index of the latter is slightly higher and averages 1.376.

If the anterior chamber is artificially emptied, it fills up rapidly with fresh fluid which is not, however, quite the same as the normal one, inasmuch as it contains a greater amount of proteid matter. But about six hours after evacuation the content of the chamber has all the properties of normal aqueous fluid. The origin of the aqueous humour has been, and is still much discussed. According to most authorities, the ciliary processes are the anatomical structures which secrete it.

In the body generally, the lymph occupying lymphatic spaces may be regarded as playing to a certain extent a mechanical part, inasmuch as it facilitates the movements of various organs, yet the function of the lymph is pre-eminently a nutritive one, its mechanical duties being comparatively insignificant. As regards the eye, the case is different, the lymph circulating in the lymphatic spaces of the eye having a double importance inasmuch as it does not only, as elsewhere, assist in maintaining the nutrition of the various tissues, especially those deprived of blood-vessels, but it also helps in a mechanical way to make the eye an adequate dioptric instrument by keeping the intra-ocular tension up to the proper level in order that both the refracting surfaces and the retina may retain their relative positions, that the movements of the pupil may not be irregular and uncertain, and that the delicate rotations of the eye under the action of the extrinsic muscles may be nicely regulated.

**The Filtration Angle or Iridic Angle.**

As already stated, the aqueous chamber may be regarded as a large lymph space, or more exactly a lymphatic cavity, though the aqueous fluid differs from ordinary lymph, inasmuch as it contains much more water and less proteid or albuminous matter. Like the serous fluid or lymph contained in the lymph spaces of the body generally, the aqueous fluid comes and goes; the particular fluid which at a given moment is present in the eye, has not always been there, some of the fluid passing away and fresh fluid continually arriving. As already stated, if the fluid is withdrawn from the anterior chamber by puncture of the cornea, the chamber is soon refilled. Indeed, under certain circumstances, a considerable quantity of fluid may be drained

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away from the chamber, fresh fluid taking the place of that which escapes. Though, under normal conditions, the quantity of aqueous humour is fairly constant, the fluid may be in excess or may be deficient, and the one phase may pass into the other. The question therefore arises: Whence comes the fluid and whither does it go?

The aqueous fluid is secreted by the ciliary processes, and perhaps by the posterior surface of the iris. This is shown by the fact that if a solution of fluorescein (which can be detected by the greenish tint it gives to the tissues it permeates) is injected into the subcutaneous tissue, not only does it speedily appear in the aqueous humour, but the ciliary processes and the peripheral parts of the inside surface of the iris are the parts of the eye in which its presence may be first detected.

The fluid thus furnished by the ciliary processes makes its way in the first place into the posterior chamber, but, though the iris lies close on the lens, there is undoubtedly a communication between the two chambers sufficiently free to allow the fluid to pass readily from one to the other, and so to fill the anterior chamber from the posterior.

There is no doubt that some of the lymph with which the sponge-like stroma of the iris is laden does find its way directly through the anterior surface of the iris into the anterior chamber, and such a transit is no doubt facilitated by the continual changes in the size of the pupil. As, however, the area of the ciliary processes is very large as compared to that of the iris, we may conclude that the greater part of the aqueous fluid is secreted by the ciliary processes, the iris contributing to a small extent.

The answer to the question, "How does the aqueous humour leave the anterior chamber?" does not present any difficulty, if the anatomy of the filtration angle or iridic angle is clearly understood. Near its circumference, the elastic lamina of the cornea or Descemet's membrane breaks up into bundles of fibres which give attachment to the iris around the angle of the anterior chamber. To these radiating and anastomosing bundles of elastic fibres, the name of ligamentum pectinatum has been given by Hueck, although some anatomists call them the pillars of the iris. (See fig. 21 and stereogram XI.) The bundles of the ligamentum pectinatum are covered with endothelial cells continued from the endothelium of the anterior chamber, but this covering does not stretch across the intervals between the bundles, so that the cavity of the aqueous chamber is prolonged into and freely communicates with

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spaces between the bundles of the pectinate ligament. These spaces are much larger and more distinct in some animals than in man; they have received the name of the spaces of Fontana. A similar but rather larger space is found immediately in front of the pectinate ligament in the substance of the sclerotic, close to its junction with the cornea. This circular space, elliptical in section, is termed the canal of Schlemm or sinus circularis iridis.

The spaces of Fontana and the canal of Schlemm are really lymphatic spaces, and it follows from the above description that the anterior chamber, at the iridic angle, communicates with these spaces which, in their turn, are in direct communication with the radicles or fine branches of the anterior ciliary veins. Since the ciliary muscle pulls on the tissue surrounding the canal of Schlemm it is possible and even probable that the movements of accommodation help alternately to close and open the canal and thus to pump its contents into the veins. By this means, the exit of fluid from the anterior chamber is rendered less dependent on the relative pressures of the blood in the veins and of the fluid in the anterior chamber. By this channel the aqueous fluid gains a ready, relatively direct and short access to the blood stream, and clinical experience shows that if this way is blocked (as happens when the filtration angle is more or less closed either by the iris being pushed forwards or by the pupil being dilated) an accumulation of aqueous fluid results which increases the intraocular tension; this may give rise to the condition termed glaucoma.

To resume, the aqueous chamber is a reservoir intercalated in a stream of fluid which is passing from the ciliary processes through the small posterior and the larger anterior chamber, the spaces of Fontana and the canal of Schlemm into the venous system. This reservoir on the one hand serves a mechanical purpose in preserving the shape of the eyeball and in affording an adequate fluid bed for the movements of the iris and on the other hand, by bringing new food materials and carrying away waste products, enables the lens and the cornea to carry out the slow and scanty metabolism necessary for the life of these structures.

**The Vitreous Body**

We have seen in the paragraphs devoted to the Embryology of the Eye that in the early stages of development of the globe the mesoderm which passes into the cup-like structure formed by the secondary optic vesicle ultimately becomes a jelly-like material known as the vitreous humour or vitreous body. In the adult state, this consists

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of a skeleton of transparent collagenous fibres arranged in irregular bundles and lamellæ, the meshes of which are occupied by a fluid very similar to the aqueous fluid, i.e., made chiefly of water with a minute proportion of organic and inorganic solid matter in solution. A few branching cells as well as wandering leucocytes (white blood corpuscles) are found in the vitreous. Where it is in contact with the retina, the vitreous body is defined by a structureless membrane, the hyaloid membrane (see stereogram VIII.) which is adherent normally to the overlying retina. At the ora serrata, this hyaloid splits into two layers, one of which is continued forward as an anterior covering for the vitreous while the other forms an independent faintly fibrillated, inelastic membrane, the suspensory ligament which is attached to, and becomes fused with, the capsule of the lens. This membrane adheres closely to the ciliary part of the retina for some distance, and some anatomists regard it as really arising from the cells of this region and not as a continuation of the hyaloid membrane.

During life the vitreous is in contact, not only with the posterior surface of the lens, but also with the back surface of the suspensory ligament. After death, however, through changes in the vitreous, a space is developed, triangular in section, between the suspensory ligament, the vitreous and the edge of the lens; this is often spoken of as the canal of Petit. According to some authors (and this opinion seems to be generally adopted nowadays) the canal of Petit exists during life, and possesses a kind of wall which is formed by the anterior continuation of the hyaloid membrane defining the front of the vitreous. As we shall see presently, it has been asserted that the capsule of the lens is imperfect behind, and if so there must be something in the nature of a membrane in front of the vitreous since, when the lens is removed from its capsule, there is no escape of vitreous into the vacant cavity. Since the suspensory ligament is attached on the outside alternately to a projecting ciliary process and to the depression between this process and the next one, the canal of Petit, when distended with air by blowing into it, has a beaded or sacculated appearance. When the canal is thus blown out, the suspensory ligament and its attachment are rendered very obvious; the ring thus formed by the suspensory ligament around the lens is sometimes called the zonule of Zinn.

For mechanical purposes the due condition of the vitreous body is perhaps more important than that of the aqueous. We have already stated that the vitreous is a structure of mesodermic origin which, in the adult, consists

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of a trabecular skeleton of collagenous or connective substance (i.e., of a substance which yields gelatine by boiling) in the meshes of which is a fluid having approximately the same physical and chemical properties as the aqueous fluid. It is generally held that the vitreous humour is also a secretion from the ciliary processes, though nothing definite is known as to the circulation and absorption of this fluid. It is assumed that it circulates and is renewed exceedingly slowly, and there is experimental evidence that the vitreous, or more exactly the trabecular portion of the vitreous, forms a sort of mesodermic sponge through which is continually streaming, though at a slow rate, a fluid identical or nearly so, to the aqueous fluid. Through the optic disc, the fluid of the vitreous has access into the lymph spaces of the optic nerve; this is shown by the fact that coloured material injected in the sheath of the optic nerve finds its way through the optic disc into the vitreous humour and passes along the central or hyaloid canal which remains in the adult after the disappearance of the central artery of the vitreous.

The greater part of the fluid of the vitreous seems, however, to follow the same path as the aqueous fluid. Fluids pass readily through the suspensory ligament, as is shown by the fact that a coloured liquid injected into the vitreous appears very soon in the anterior chamber. Moreover, a blocking of the iridic angle leads to undue distention not only of the anterior and posterior chambers but of the whole globe of the eye if such a blocking occurs at an early period of life, when the sclero-corneal coat has not yet acquired the rigidity it possesses at the adult stage. Finally, the pressures in the aqueous and vitreous fluids are always the same, and vary similarly and concurrently.

We have no evidence that any large amount of fluid passes directly from the choroid through the retina, past the internal limiting membrane and the hyaloid membrane into the vitreous. As far as we know, the whole of the lymph in the retina is carried away through the lymph spaces of the optic nerve, and we must therefore conclude that the region of the zonule of Zinn serves as the door both for the entrance and the exit of the fluid, its circulation through the vitreous between the fibres and laminæ of the trabecular skeleton being secured by diffusion assisted by the movements of the eyeball.

**The Intraocular Pressure.**

The pressure in the eyeball is, as will be readily understood, one of the most important factors in the proper working of the dioptric system of the eye. The tension of the

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globe depends: (a) on the pressure of the contents; (b) on the resistance opposed by the more or less elastic tunics. As the latter is constant, or at any rate varies but little within physiological limits, we must, in order to understand the oscillations of intraocular pressure, consider the factors which determine the amount of fluid contained in the eye and the pressure existing in the intraocular blood-vessels. Normally, the height of intraocular pressure varies, in man and in the higher animals, between 20 and 30 mms. of mercury. The methods used for the measurement of the intraocular pressure are of two kinds. Manometers (for experimental work in the laboratory) and tonometers, for clinical purposes. The former are brought into communication with the interior of the eye by means of special cannulæ and the pressure is read on the manometer tube. A tonometer is an instrument by which a small plate exerts a pressure on the outer wall of the eyeball so as to flatten it. By measuring the force necessary to obtain a certain degree of flattening, it is easy to calculate the pressure within the eye. Broadly speaking, the intraocular pressure rises and falls with the general blood pressure; the dim cornea and sunken eye that betoken approaching death are due to the fall of blood pressure which occurs towards the end of life. The fact that oscillations of intraocular pressure correspond to those of the blood pressure is evidenced by the pulsation of the retinal vessels when the intraocular pressure is high as is the case in glaucoma.

**The Crystalline Lens.**

The crystalline lens, together with its suspensory ligament, lies between the iris and the vitreous body. It assumes the form of a biconvex, transparent lens which lies within the circle formed by the ciliary processes, but in such a way that its equatorial margin is distant about half a millimetre from the apices of the processes. The interspace between the ciliary body and the equator of the lens is termed the circumlental space. The posterior lens surface is fitted into a hollow depression of the vitreous body (or fossa patellaris). As the vitreous body is practically incompressible, the curvature of the posterior lens surface can hardly alter, and its radius of curvature in the average human adult eye is about 6 mms. The anterior surface, on the other hand, is immersed in the aqueous fluid and can alter its curvature under the effect of the ciliary muscle. The radius of curvature of this surface averages 10 mms. when the ciliary muscle is in a state of physiologic rest, but

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can reach a value of 6 mms. when the ciliary muscle is fully contracted in the case of a young subject, e.g., a child of 10 years of age.

The lens, as a whole, is kept in its position by the suspensory ligament or zonule of Zinn, the arrangement of which is shown in fig. 21 and in stereogram VII. The sagittal diameter (or thickness) of the lens is about 4 mms. in the adult and the equatorial diameter averages 9 mms.

The body of the lens is enclosed in a transparent sac called the capsule, and the lens substance itself is made of a central core or nucleus surrounded by a softer and more elastic portion called the cortical part or the cortex. In a normal eye, the cortex is colourless, while the nucleus has a slight yellowish hue. The nuclear part of the lens owes its greater consistency and also its coloration to a process known as sclerosis (or hardening) which mainly consists in a gradual loss of water. The sclerosis begins even in childhood, but advances so slowly that it is not till the age of twenty-five that a distinct though still small nucleus is present. Since sclerosis of the lens fibres is a change due to advancing age, it affects first the oldest fibres, i.e., those which lie in the centre, and as the process advances, the nucleus steadily increases in size at the expense of the cortex, which diminishes correspondingly, so that, at an advanced age, almost the entire lens is converted into nucleus, i.e., is entirely sclerosed. There are many individual differences in this regard, so that persons of the same age have lenticular nuclei of different sizes. The size of the nucleus is of practical importance in the operation for cataract.

The sclerosed portion of the lens is hard and rigid and incapable of changing its shape. Hence, the further advanced the sclerosis of the lens is, the less capable it is of making those alternating changes in curvature which are necessary for the function of accommodation. For this reason, the accommodative power of the eye diminishes with advancing age; this results in a recession of the near point and, ultimately, in the production of the condition called presbyopia.

The nucleus reflects more light than the non-sclerosed part of the lens and, for this reason, the pupil of an elderly person whose lens has a large nucleus is no longer of such a pure black as in youth. It gives a grey or greyish green reflex (the senile reflex) which is often confused by the inexperienced with a beginning of cataract.

The external envelope of the lens or lens capsule is a homogeneous membrane slightly thicker on the anterior than on the posterior surface. The anterior portion is further

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distinguished by having a single layer of cubical epithelial cells, the lens epithelium, which plays an important part in the growth of the lens, as the fibres of the latter originate from the cells of the capsular epithelium. On following the epithelium towards the equator we see that the epithelial cells become taller and longer until they are converted into long fibres, the fibres of the lens. As these originate from the meridional rows of epithelial cells, they arrange themselves in radiating lamellæ, and this explains why opacities in the lens so often occur in the form of radial striæ. As the epithelial cells become elongated, their nuclei recede from the capsule into the interior of the lens so that a zone is found along the equator in which there are numerous nuclei lying in the lens substance. This nuclear zone, as it is called, represents the portion of the lens in which the growth of the latter takes place. This growth occurs by a process of apposition, new epithelial cells constantly growing out into the lens fibres which are placed next to, and outside of, the older fibres. In this way the lens acquires a concentrically laminated as well as a radial structure, the fibres lying in the central portion being the oldest, while the most external ones are the youngest. The reason for cell-nuclei not being present outside the nuclear zone in the interior of the lens is that the nuclei disappear from the older lens fibres.[1]

The fibres constituting the lens have the form of long, prismatic six-sided cords; they are closely applied to each other, forming concentric laminæ arranged somewhat like the coats of an onion, and are held together by a cement-like substance. The lamellæ of the lens are seen in stereogram XIV. See also the chapter on Dissection (page 363). The fibres begin and end upon the anterior and posterior surfaces of the lens along lines which radiate from the anterior and posterior poles; here they form a Y-shaped figure, the stellate figure of the lens, which can often be recognised in the living eye of adults by focal illumination. The three rays of the stellate figure alternate in position on the two surfaces, thus dividing the lens into six sectors whose apices meet in the region of the anterior and posterior poles. In pathological cases (e.g. in opacities of the lens) the sectors often stand out very prominently. The fibres of the nucleus can often be distinguished from those of the cortex by being more slender and having edges which, owing to the shrinking of the fibres, are finely serrated; there is, however, no sharp line of distinction between the nucleus and the cortex.

[1] Fuchs's "Text-Book of Ophthalmology," pages 522, 523.

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The structure of the lens will be better understood if we consider its embryological development. We have seen that the lens springs from the outer or superficial ectoderm of the embryo which becomes invaginated (i.e. folded in) to form the lens vesicle. The coating of cells upon the posterior wall of the vesicle grows out and is used up to form the lens fibres and thus, later on, when the lens is completely formed, there are no epithelial cells left on this wall. By this outgrowth of cells and their transformation into long fibres, the whole vesicle is filled up so as to form a solid body in which each one of the newly formed fibres extends from the anterior to the posterior lens capsule.

The subsequent growth of the lens by apposition of new fibres continues, as is the case in all other epithelial structures, during the entire life. But while in other epithelial structures (e.g. epidermis, hair, nails) the exfoliation (i.e. the shedding) of the oldest cells serves to maintain a state of equilibrium, no such exfoliation is possible in the lens which is completely shut in, and compensation takes place by a diminution in the volume of the oldest fibres through a process of shrinking resulting in the formation of the nucleus. This diminution in volume does not, however, fully offset the growth of new fibres and the lens therefore keeps on enlarging even in advanced age. According to Priestley-Smith, in the sixty-fifth year of life, its volume is about one-third more than in the twenty-fifth year.

The lens subserves optical purposes exclusively and as its optical functions are not associated with consumption of matter, nutrient materials are required in the lens only in extremely small quantities in order to keep the capsular epithelium and the lens fibres from dying. This nutrient material the lens receives from the surrounding fluids, the vitreous and mainly the aqueous, by diffusion through the capsule. Definite, preformed, channels for the circulation of liquid within the lens do not exist. That the metabolism of the lens, very much like that of the cornea, goes on with extreme slowness is proved by the fact that pathological processes (for instance opacities) often remain stationary for an uncommonly long period or spread but very slowly.

In another respect the lens is more or less similar to the cornea. The lens fibres, like the fibres of the cornea, have the property of absorbing liquids in considerable amount and consequently of swelling up and becoming opaque. If, after opening the capsule, we place the lens in water, or if, in the living eye, we give the aqueous fluid access to the lens fibres by cutting the capsule open, the lens

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becomes cloudy and swollen. We may ask by what means, in normal conditions, the lens is protected from the entrance into it of the aqueous. Just as in the cornea it is not Descemet's membrane but the endothelium that keeps the aqueous back, so in the case of the lens, it is not the capsule, but mainly the epithelium of the latter that effects the same object. Hence, every lesion of the capsular epithelium leads, sooner or later, to cloudiness of the lens. Thus are explained not only traumatic cataracts with ruptures of the capsule, but many other sorts of cataracts in which the epithelium is injured without rupture of the capsule. This behaviour of the lens is made use of in the procedure of rendering a partially clouded lens completely opaque (artificial ripening). This operation consists in massage of the anterior lens surface (through the cornea) so that the capsular epithelium be injured by compression. Another form of clouding of the lens is observed if the composition of the aqueous or vitreous is essentially altered or poisonous substances are present in these fluids. Thus are explained the opacities of the lens depending on poisoning (e.g., naphthalinic cataract) and also most cases of complicated cataracts in which, by disease of the inner coats of the eye, an essential change is set up in the aqueous or vitreous.

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# CHAPTER XII.

## DESCRIPTIVE ANATOMY OF THE NERVOUS APPARATUS OF THE EYE, RETINA, OPTIC NERVE AND VISUAL CEREBRAL CENTRES.

**The Nervous Apparatus of the Eye.**

The macroscopic study (i.e., the study by means of dissection and examination with the naked eye by contradistinction with microscopic study) does not give definite indications on the disposition of the nervous apparatus of the eye, nor does it show anything definite about the intracerebral path of the optic fibres, but it shows the general arrangement and must necessarily be the starting point for a more accurate investigation.

A complete study of the nervous apparatus of the eye should be carried out first by examination with the naked eye (or with a simple magnifying glass when necessary), with the ophthalmoscope, with the microscope, and finally by the anatomo-clinical method.

At a first glance, descriptive anatomy shows that from the posterior part of the globe an optic nerve proceeds, passes from the orbit into the skull and partly unites with its fellow to form the chiasma from which the two optic tracts spring. Each optic tract seems to become part of the corpora geniculata (internal and external) which are, in their turn, connected with the corpora quadrigemina.

This is all we can do by means of dissection. In fact, up to recently, anatomists used to regard the corpora geniculata and quadrigemina as the real origin of the optic nerve. It is true that, in 1846, Gratiolet described a cerebral expansion of the optic tracts which he called the optic radiation, but he thought that the fibres forming this expansion radiated in the whole extent of the cortex of the cerebral hemispheres. By methods we shall examine presently, it has been found that the fibres forming the optic radiation are directed to the cerebral cortex about the internal part of the occipital lobe near the calcarine fissure.

To sum up, dissection and examination with the naked eye only enable us to trace the path of optic fibres from the retina to masses of grey matter constituting the ganglia of the base of the brain (corpora geniculata and corpora quadrigemina). These ganglia are termed the primary visual centres.

Let us examine this portion of our subject a little more deeply, going from the retina towards the brain. The



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opposite way is generally adopted in text-books, but the former is more logical as it represents the direction of propagation of visual impulses.

**The Retina.**

It is easily ascertained that if a human eye is cut by a section perpendicular to the visual axis, the internal portion of the posterior half of the globe, especially if the vitreous body is carefully removed, appears with a brownish background formed by the choroid, over which a transparent membrane, the retina, can be made out. This retinal membrane, transparent if the eye is freshly removed, soon becomes opalescent and it can be seen that it apparently covers the posterior two-thirds of the ocular cavity and extends forwards to an indented border, the ora serrata, situated a little farther back than the ciliary processes. The nervous or physiological retina ends at the ora serrata, but really the retinal membrane is continued forwards up to the pupillary margin by what are termed the ciliary and the iridic parts of the retina, as we have stated before. Besides the blood-vessels which run in it, as we shall see a little later, the retina presents two important regions which can be recognised with the naked eye, namely the macula or yellow spot and the papilla or optic disc.

On a retina that is still transparent the macula appears as an oval darkish-brown spot with its major axis (about 2 mms. long) either horizontal or slightly oblique. The macula is near the posterior pole but slightly on the temporal side of it and may be regarded as the physiological centre of the retina.

The papilla or optic disc (1½ to 2 mms. in diameter) is lighter than the choroidal background, and the retinal vessels radiate from it. The disc represents the region where the optic nerve is continued into the retina. It is about 4 mms. (inward) from the macula and 1 mm. above it.

Let us now examine the different regions of the retina, first with the naked eye, with the aid of a magnifying glass, if necessary, and with the ophthalmoscope.

The ora serrata, as already mentioned, is the black indented line forming the anterior limit of the physiologic retina. It is shown most distinctly in stereogram IV. and consists of two parts: (*a*) The indented border itself, that is the line made of angles directed alternately in and out; this disposition is not regular, the sinuosities are deeper on the nasal side and diminish toward the two extremities of the vertical diameter; they are hardly visible on the external side. There are in the ora a variable number of teeth,

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ranging from 18 to about 40, the width of each varying from ½ to 2 mms; the ora serrata is less marked in children. (*b*) A brownish zone about 1 mm. wide immediately behind the indented border. It is in this zone that the adherence of the retina to the choroid begins. This adherence becomes perfect on the indented line, the physiologic retina being continued into the ciliary part of the retina which forms the epithelium of the ciliary processes.

When the retina undergoes post-mortem changes, and becomes opalescent, it forms at the level of the ora serrata a kind of projecting circular ring which clearly shows the end of the physiologic retina.

The microscope is necessary to show the structural or histological differences between the retina proper or physiologic retina and the ciliary and iridic parts of the retina. We shall revert to the subject a little later. The ophthalmoscope cannot give a view of the ora serrata, but this part, as well as the ciliary part, is well displayed in stereogram IV.

The naked eye examination of a fresh retina in an open eye shows it to be absolutely transparent and to allow a view of the pigmented layers below it, the brownish shade of these layers varying in subjects and races. The retina itself is only visible by its blood-vessels. The same remark applies to the ophthalmoscopic examination but then, owing to the high magnification (12 to 15 in the direct method) there is a special "granite" appearance due to small pigmentary irregularities of the epithelial layer. The ophthalmoscope also permits a differentiation between the arteries (vivid red) and the veins (darker and usually thicker). In children and young subjects the retina shows a "shot" appearance, especially in the neighbourhood of big vessels; this is probably due to a raising of the anterior surface by the vessels; inclined surfaces are thus produced, hence the play of light.

The macula is best studied with the ophthalmoscope in children. It shows as a dark oval patch (long axis usually horizontal) on the reddish ophthalmoscopic background. The short axis (vertical) appears about equal to, or slightly less than, that of the papilla (1½ mms.). The long axis (horizontal) is about 2 mms. This dark oval is surrounded by a delicate luminous reflex, a minute bright spot at the centre is surrounded by a zone even darker than the macular area itself. These luminous effects, or retinal reflexes, are explained (like those seen along vessels) by differences of level: the macula is a slightly depressed surface with a still deeper depression at the centre (fovea) as shown in microscopic sections; the light sent by the mirror is reflected by the inclined surfaces thus formed. In the adult the peripheral

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macular reflex disappears but the foveal one often remains visible, at least in the examination by the direct method.

On an open eye, the retina of which is fresh and transparent, the macula only shows as a small dark brown spot, badly defined and in which no details are visible, but after a few hours, when the retina has become opalescent and somewhat œdematous, the macula assumes a light yellow colour (hence the name of macula lutea). At the centre of the spot, the post-mortem thickening of the retina renders the foveal depression very apparent. In fact, the fovea is deeper than in the living eye because at this point the retina is very thin and does not undergo the same thickening as the rest of the macula.

The dark brownish shade of the macula when the retina is *in situ* is especially marked round the fovea. This dark appearance is due to several causes: the chief one is the high pigmentation of the subjacent hexagonal epithelium. Moreover, this epithelium is seen through a modified, thinner, retina showing distinctly the dark coloration of the pigment. Finally, the macula possesses a straw coloration of its own which cannot be seen either in the fresh (transparent) retina so long as it is applied on the choroid, or with the ophthalmoscope in the living eye. In both cases, the proper colour of the macula is not visible on the dark background formed by the subjacent tissue which is viewed by transparency. But after death, when the retina becomes opacified and no longer allows the choroid to be viewed, then the true colour of the macula becomes apparent.

If the retina, still transparent, is detached from the choroid and examined by transparency on a light ground, it shows a yellow spot, corresponding to the macula and the fovea appears as a colourless spot in the middle of the yellow spot. Hence, and strictly speaking, the yellow colour of the macula is not really the result of post-mortem changes as is often stated, but it is the post-mortem opacification of the retina that makes it apparent in the retina *in situ*.

Anatomically, the papilla belongs to the optic nerve but topographically, it must be described as a part of the retinal surface. With the ophthalmoscope it appears on the choroidal background as a light patch, circular or almost circular. Its diameter is 1.5 to 2 mms. The retinal vessels proceed from near its centre. It is generally surrounded by a white border or scleral ring, which is the edge of the sclerotic hole seen through the nervous semi-transparent fibres constituting the papillar tissue. Immediately outside the scleral ring there is a second ring, often incomplete and reduced to a thin band on the temporal side; it is the

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choroidal ring, i.e., the pigmented edge of the choroid visible where it is not covered by opaque retinal epithelium.

The papillar surface has not the geometrical regularity of the rest of the retinal surface: such a regularity would be useless as the spot is blind. Yet the papilla does not form a projection as its name implies. It presents, on the contrary, a central depression, variable in size and depth, due to the spreading of the nervous fibres radiating into the retina (physiologic cup). Emerging from the nasal side of the cup and accompanied by a great number of nerve fibres, the vessels form at this point a very slight projection. At the bottom of a large physiological cup it is often possible to see the lamina cribrosa, especially with the higher magnification of the direct method. The nerve fibres, being transparent, do not show on the papilla, but, in children, it is frequently possible to see (direct method) a striation, immediately round the papilla, due to the radiation of the fibres.

**Retinal Blood-Vessels.**

The central artery and vein emerge from near the centre of the papilla, the artery being generally on the nasal side of the vein. The first bifurcation of the central artery occurs generally vertically, so that we see with the ophthalmoscope a superior or ascending and an inferior or descending artery. Each bifurcates again so as to form a temporal and a nasal branch, superior and inferior, and the bifurcation goes on dichotomously so as to cover the whole retinal surface.

The two temporal arteries (superior and inferior) curve above and below the macular region: the macula and the surrounding part are thus free from large vessels though highly vascularised by fine branches converging towards the macula. This arrangement is the result of the necessity for a physical and anatomical perfection at the macula: this perfection would be diminished by reflexes and shadows of big vessels and by occasional troubles in the circulation of these vessels.

The veins are distributed like the arteries though the venous tree is not juxtaposed to, but intercalated with, the arterial tree. That is, as a rule and except necessarily near the disc, the arteries and veins do not proceed side by side as is usually the case in the limbs and other parts of the body, but each vein is placed about the middle of the angle formed by two diverging arteries. This, again, is due to a physiologic necessity, since the juxtaposition of two vessels would form a more or less opaque band, troublesome by its shadow and reflexes.

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**Post-mortem Changes in the Appearance of the Retina.**

A few hours after death the retina becomes opalescent: its tissue swells, this swelling causing the formation in the free surface of projecting folds, the arrangement of which is constant. The first fold to appear is one going a little obliquely from the papilla to the macula: it is the plica centralis retinæ of old authors, who regarded it as normal. Other folds go from the papilla to different points of the ora serrata, but those which pass above and below the macula curve exactly as the blood-vessels do. The direction of these folds is evidently determined by that of the bundles of nervous fibres. We shall come again on this point in the part on microscopic anatomy.

**Coloration of the Retina—Visual Purple.**

The study of the coloration of the retina and of the visual purple belongs to the branch of science called Physiologic Optics. For our present purpose we shall merely say a few words on the coloration of the living retina, this coloration being more easily observed in the eyes of animals. which have been kept in the dark for some time before death.

The subject was investigated by Boll in 1876. The best eye for the study of this question is that of the frog. The animal being kept in the dark for a time before being killed, its eye is divided and the retina separated from the choroid by means of a pair of forceps; the pigment epithelium appears first of an intense red. This colour fades during the first few seconds and disappears after about 30 seconds, leaving a slight yellowish shade (1st stage). During the 30 to 60 seconds following and sometimes for a longer period, the retina shows a satiny, brilliant appearance (2nd stage). Then, this disappears and the retina becomes transparent and remains so for about 15 minutes or even more (3rd stage). After this, it becomes opaque (4th stage). Boll thought at first that this red appearance was a transient vital property which could only be demonstrated a short time after death. But, examining eyes a few seconds after the death of the animals, he found that the retina is not always red and he came to the conclusion that the absence of coloration is not due to death, that it may occur during life and that the action of light could determine the presence or absence of coloration. Examination of the retinæ of animals exposed to the sun and of others kept in the dark showed him most plainly that the former were pale, the latter red.

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Kuhne found in human eyes (bandaged for a time immediately before death or examined after 48 hours in the dark) that the retina, viewed by its choroidal surface, showed a red coloration quickly disappearing in the light. The yellow spot was not affected, and the same applies to a zone about 2 mms. wide immediately behind the ora serrata.

A clear understanding of the anatomical relation of the retina to the choroid and the vitreous is of the utmost importance. The retina is applied over the internal surface of the choroid. It envelopes the vitreous which is moulded on its concave surface. There is no actual connection between the retina and choroid, although the two membranes may physiologically present a reciprocal adherence. Boll found that in eyes conserved in the dark the retina is easily separated from the pigment epithelium, but if the eye has been under the influence of light, the separation is not so easy, the retina being often broken in the attempt. He suggested that the action of light on the pigment caused the difference and this has been verified. On microscopic sections he could see that in those eyes kept in the dark the interstices between the rods were completely free from pigment, whereas in eyes exposed to light, filaments of pigment extended from the cells of the pigment epithelium up to the bases of the rods, i.e., to the so-called external limiting membrane. Thus, the pigment cells of the pigment epithelium, which are attached by a cement-like substance to the choroid, may, by penetration of their protoplasmic filaments, determine a fairly strong adherence between the choroid and the retina.

The fact was originally observed by Boll in the frog's retina. Later on, it was found that the phenomenon is more marked in fishes, amphibia, reptiles and birds than in mammals, and Schultze has shown that it applies to the human retina, the penetration extending nearly to the bases of the rods. The pigment epithelium is therefore capable, at least under the action of light, of constituting a means of union between the choroid and the retina.

In most cases of pathological detachment of the retina the external surface is white, but then the pigment epithelium remains with the choroid, i.e., the detachment occurs between the retina and the pigment epithelium as in the case of the retina of the frog in the dark. We must not conclude, however, that the pigmentary adherence does not exist but that an alteration of the pigment cells has destroyed this adherence and prepared the detachment.

The retinal surface is kept in the regular state necessary for vision by the pressure of the vitreous, and the normal

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vitality of the latter is of considerable import to the former. If the vitreous shrinks, or becomes soft, the retina is threatened with detachment. When the detachment is complete the nervous membrane finally forms a cordon, the posterior end of which is at the papilla, the anterior end widening like a funnel, the circumference of which is fixed to the choroid at the ora serrata. The papilla and the ora are the only two regions where the retina presents adherences, these being formed by the retina being continuous with the fibres of the optic nerve on one hand and by the ciliary part of the retina (which is intimately connected with the choroid) on the other hand.

Level with the papilla, the vitreous presents the widened aperture of Cloquet's canal; the papillar surface is therefore in contact with the liquid filling the canal; this detail can only be observed on sections as, owing to the transparency of this structure, it cannot be seen with the ophthalmoscope.

The vitreous is in contact with the retina in the living eye but, after death or by maceration, the two parts become separated showing a well defined membrane (hyaloid) enclosing the vitreous. Occasionally an adherence may occur at some part of the papillar edge; this is probably due to a vestige of the central artery of the vitreous, under the form of fine connective tissue filaments not visible to the naked eye.

**The Optic Nerve.**

The nervous cord uniting the retina to the ganglia of the base of the brain forms a continuous whole. But, for descriptive purposes, we shall consider separately: the optic nerve, the chiasma, the optic tracts, and the ganglia of the base or primary visual centres.

On opening the orbit we find that the optic nerve, surrounded by its sheaths, forms a white cord, about 4 mms. thick, extending from a point near the posterior pole of the eye to the optic chiasma. It is practically cylindrical in the orbit and the optic canal: distinctly flattened vertically in the cranium.

The optic nerve may be divided into: (*a*) a short intrascleral portion (not visible): (*b*) an orbital portion (about 24 mms.): (*c*) a canalicular portion (6 to 7 mms.): (*d*) a cranial portion (10 to 12 mms.).

(*a*) The intrascleral portion measures about 1.25 mms. in length. The so-called sclerotical foramen, through which the nerve passes into the eye, consists of numerous small holes in the inner layers of the sclerotic, forming a sieve-like partition known as the lamina cribrosa. The external fibres

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of the sclerotic do not enter into the formation of the lamina but are reflected backwards and become part of the dural sheath of the nerve.

(*b*) The orbital portion presents two S-shaped curves which permit free rotation of the eye without the nerve becoming taut.

(*c*) The canalicular part of the nerve lies in the optic canal which consists of a bony portion, 4 mms. in length and of a fibrous portion extending into the cranial cavity for a distance of about 2 to 3 mms. Only the nerve and the ophthalmic artery (which lies on the inner side of the nerve) pass through the canal; the nerve, surrounded by its sheath which adheres to the periosteum, exactly fills the canal; hence, a traction, however violent, is not transmitted to the brain but owing to the fact that the optic nerve within the canal is tightly enclosed by the bony wall of the latter, this portion of the nerve, like the intrascleral portion, has a peculiar predisposition to morbid affections.

(*d*) The intracranial portion of the nerve extends from the end of the optic canal to the chiasma; it is practically straight. It is subject to pressure from intracranial tumours and to constriction from organised inflammatory exudates.

The optic nerve forms a homogeneous trunk, surrounded by sheaths. In the short intrascleral portion, the nerve is compressed in the scleral ring: beside, it appears translucent but becomes white and opaque and increases in volume as soon as it emerges from the posterior scleral surface. These two modifications are due to the fact that on passing into the globe the myeline sheath surrounding every optic nerve fibre in the orbital and intracranial portions of the nerve is discarded; this accounts for the sudden decrease in the diameter of the nerve as it passes through the lamina cribrosa since its constituting fibres are now reduced to the thickness of thin, bare, and transparent cylinder-axes.

With the naked eye, the nerve appears as made of a single bundle or, more exactly, it is not divisible by dissection into secondary bundles as is the case for nerves in the limbs. It is firm; its tissue is extremely strong and cannot be crushed between the fingers. The pia mater is embodied in the surface of the nerve, and on attempting to separate the two by dissection, it is found that the former (pia mater) sends into the thickness of the nerve a quantity of partitions or septa which give it its firmness and strength. In the orbital part the nerve is surrounded by a white, fibrous, thick envelope continuous with the sclerotic on the one hand and, through the optic canal, with the cranial dura mater on the

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other. This envelope is called the dural sheath, which strongly adheres to the tendons of insertion of most of the ocular muscles at the orbital end of the optic canal, as we shall see later on. In the canal itself it adheres to the periosteum and, in this way, it forms the chief insertion of the optic nerve at the apex of the orbit; in fact, a strong man pulling on the globe with all his strength could not drag it out of the orbit. It follows that a traction, surgical or traumatic, is not transmitted to the brain; it stops at the optic canal. In the cranium, the nerve is no longer covered by its dural sheath as this, at the posterior end of the optic canal, is continuous with the dura mater which lines the cavity of the skull. The pia mater covers this part of the nerve in the way already described.

**The Optic Nerve Sheaths.**

To resume, the three sheaths of the optic nerve originate from the three membranes enveloping the brain. The inner one or pia mater closely embraces the trunk and from it, bands of connective tissue or septa pass into the interior of the nerve: with them pass the blood-vessels. The external (dural sheath) is much thicker than the internal one and surrounds the nerve loosely in its orbital and canalicular portions. Owing to this, a fairly broad space (intervaginal space) is left between the pial and the dural sheaths. The middle or arachnoid sheath is a very delicate pellicle which is united by numerous trabeculæ of connective tissue to the external and internal envelopes. It divides the intervaginal space into two portions, the subdural and subarachnoidal spaces, which communicate with the cerebral spaces of the same names. These appear particularly prominent when they are pathologically dilated by an accumulation of fluid, as in optic neuritis. The surfaces of the sheaths adjacent to these spaces are provided with an endothelial coating, so that the subdural and subarachnoidal spaces are lined completely with endothelium, and must be regarded as true lymph channels.

Anteriorly, the three sheaths become united to the sclerotic. The external and middle sheaths pass into the outer two-thirds of the sclerotic: the inner sheath goes to the innermost lamellæ of the sclerotic which form the lamina cribosa, and it is also connected with the choroid. The intervaginal space has a blind ending situated within the sclerotic. Posteriorly, the three sheaths are continuous with the corresponding membranes of the brain.

The blood-vessels necessary to sustain the life of the optic nerve pass from the pia mater into the nerve. In addition,

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in the anterior portion of the orbital section there are found the central vessels of the optic nerve. The central artery is a branch of the ophthalmic artery: the central vein empties into the superior ophthalmic vein or directly into the cavernous sinus (see page 335). Both vessels enter the optic nerve ten to twenty millimetres behind the eyeball and run in the axis of the nerve as far as the papilla, where they divide into the retinal vessels which have already been described.

**The Optic Chiasma, the Optic Tracts and the Primary Visual Centres.**

The chiasma is formed by the meeting of the two optic nerves which seem to be fused to form a thick nervous plate, the posterior angles of which give birth to the optic tracts. Partly embedded in the cerebrum, and well visible on a brain turned upside down, the chiasma appears as a white quadrilateral plate with concave sides, wider than long (12 to 14 mms. wide; 5 to 6 mms. long). The inferior surface of the chiasma lies in the optic groove of the body of the sphenoid bone; most of the superior surface projects into the cavity of the third ventricle. Dissection is insufficient to elucidate the course of the optic fibres in the chiasma.

The visual or optic tracts can only be seen on a fresh brain when the anterior part of the cerebral lobe has been raised (or cut away on a hardened brain). Each tract appears as a flattened white bundle extending from the posterior angle of the chiasma to the geniculate bodies. The tract passes round the cerebral peduncle and, near its end, it divides into two roots, each of which is continuous with one of the geniculate bodies. (These bodies are, as we have seen, two small rounded masses of grey matter on each side of the median line, under the pulvinar or posterior part of the optic thalamus). The external root of the optic tract goes to the external geniculate body, the one forming a projection from the inferior surface of the pulvinar. The internal root, smaller than the other, goes to the internal geniculate which is smaller than the external and placed nearer to the median line. According to recent researches, the internal root of the visual tract and the internal geniculate body are not concerned with vision.

The quadrigeminal bodies are so called because they consist of four rounded masses of grey matter situated under the corpus callosum above the aqueduct of Sylvius. They are arranged in two pairs on each side of the median line, the anterior pair and the posterior pair. The anterior quadrigeminal bodies appear as two ovoid masses of greyish shade, 8 to 12 mms. long; from the external part of each

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a white cord, termed the arm of the corresponding body, connects it with the external geniculate on the same side of the median line.

**The Cortical Visual Centre.**

The geniculate bodies and the quadrigeminal bodies were formerly regarded as being the real origin of the optic nerves. It is well known now that such is not the case: only the external geniculate and the anterior quadrigeminal on each side of the median line belong to the visual apparatus. They constitute the infra-cortical centres or, as often termed, the basal or the primary visual centres; they represent an association of sensory centres, motor centres and conductors connecting these various centres, but they do not represent the true visual centre which is located in the brain cortex and is necessarily connected with the primary centres. This connection is intracerebral and cannot be ascertained by mere dissection and examination with the naked eye or even with the microscope. It is true that Gratiolet described (1846) a system of fibres extending in fan-like fashion, from the primary centres to the cortex, but he thought that this optic radiation, as he called it, was distributed to the whole of the cerebral cortex. It was in about 1880 that physiologists began to localise the visual centre in the occipital lobe. The exact limits are not absolutely determined, but, as we shall see later on, it is certain that the calcarine fissure and the convolutions which are above and below it, namely the cuneus above and the lingual lobe below, are parts of the visual centre. In fact, this centre seems to extend to the whole of the internal surface of the occipital lobe, especially to the part about the calcarine fissure.

**Comparison of the Nervous Apparatus of the Eye to that of other Sense-organs.**

A brief comparison of the nervous apparatus to that of other sense-organs and a few supplementary remarks on the embryological development of the retina will be of some help to enable the reader to gain a sound knowledge of the present part of our subject.

The retina, like all other parts of the bodies of living beings, is the result of an embryological evolution or development which is but the repetition in an exceedingly short time of the infinite series of ancestral states. In order to understand the why of the present state, we must therefore have some knowledge of the ontogenic and phylogenic past.

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(Ontogeny is the development of the individual, phylogeny, that of the species.) Moreover, the retina is part of a family of organs (sense-organs), the mechanisms of which are very similar, as we have already pointed out (page 135). It follows that the simplest of these organs give to some extent the key to the working of the more complicated ones, amongst which is the retina. Finally we find in the animal series (in mollusca, pineal eye of some reptiles) retinæ which, though simpler in structure than the human retina and differing from it by their origin and development, are, however, essentially similar and the study of these simpler forms is calculated to furnish important data concerning the retinæ of higher vertebrates. Hence we will proceed to a brief study of the following subjects. (a) General anatomy of sense-organs. (b) Embryological development of the retina. (c) Comparative anatomy of the retina.

**General Arrangement of the Sense-organs.**

Let us explain first the analogies of the retina with the nervous parts of other sense-organs. We have seen that the nervous system is essentially made of nervous cells and nervous fibres. It has been recently ascertained that these two elements are not independent and that a nervous fibre is never found except as a process emanating from a nervous cell. The term "neuron" is used to denote a nervous cell and all its processes (dendrites and axon). We have seen that nerve cells are of different shapes, often irregular in form and varying in size from 6 to 60 microns. A typical nerve cell consists of a nucleated mass of protoplasm from which processes extend; cells are termed uni- or bi- or multi-polar according to the number of their processes. Most of these processes break up into branches but one of them is distinguished by not branching. The branching processes are termed dendrons or dendrites and the unbranched one, which is continuous with the axis-cylinder of a nerve-fibre, is termed the axon. Each cell with its dendritic processes and its axon is an independent structure, a neuron, the connection of one neuron with another being made by the adjoining of the processes. In other words, neurons are not anastomosed but simply juxtaposed and the transmission of impulses from one neuron to another does not occur through continuity of substance but because the protoplasmic processes of one are in contact with those of the other. In fact, the nervous system is made of neurons which are articulated with each other, these articulations or synapses, as they are termed, establishing a physiologic though not an anatomical or structural continuity.

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In the dendrons or dendrites, the direction of the impulses is cellulipetal; it is cellulifugal in the axons. The dendrons are therefore receivers of impulses produced in neighbouring elements; they transmit these impulses to the cell to which they belong. The axon, on the other hand, transmits the impulses produced in the cell to the elements with which it is connected (Van Gehuchten's law of the dynamic polarisation of nervous elements).

All sense-organs are formed of epithelial surfaces, of ectodermic origin, each of which is modified in view of its adaptation to a special function and is connected with the central nervous system by a chain of neurons.

Though apparently very different, all the sense-organs are built on the same principle, as we have seen before. The sensitive neurons, in which the nervous current flows from the periphery towards the centre, present ramified processes in relation with the sensorial epithelium and a cylinder-axis process directed towards the cerebro-spinal centres.

In the simplest type of sense-organ, that of touch, the sensitive neuron is located in the skin and is connected by an intermediate neuron with a central neuron in the cerebro-spinal centres. In more complicated sense-organs, we find that the sensitive or peripheral neuron and the central or perceiving neuron are connected by intermediate neurons which form a chain, the various elements of which have a tendency to become more closely associated, an arrangement which is evidently an improvement permitting an easier, quicker and more perfect working.

In the retina, these new conditions are realised to a high degree. As we shall see presently the retina includes the sensorial epithelium or peripheral neuron, an intermediate neuron and a central neuron, arranged in a series perpendicularly to the thickness of the membrane. It also includes other neurons, not belonging to the fundamental chain, but disposed horizontally in order to connect together the various elements of a same retinal layer.

These considerations show that the retina is a true nervous centre since it includes in its thickness not only the sensoral epithelium and the peripheral neuron, but also the central neuron. As we shall see presently, embryology confirms this view: it shows that the retina is not developed as an independent organ but as an expansion of the brain. Besides, the retina contains a substance, termed neuroglia, which is only found in nervous centres. It follows that the optic nerve is not comparable to an ordinary, peripheral, nerve but is really a commissural nerve connecting two nervous centres.

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**Embryological Development of the Retina.**

In our brief study of the embryological development of the eye (page 141) we have shown that, at an early period, the anterior cerebral vesicle of the embryo gives rise on each side to a hollow outgrowth which increases in length and becomes thinner at its base (embryo optic nerve). It dilates at its free extremity so as to form the primary optic vesicle. In this vesicle, spherical in shape, we can consider two hemispheres, the proximal one, near to the brain, and the distal one.

The distal hemisphere flattens, then becomes concave and finally penetrates into the cavity of the proximal hemisphere. When this invagination is complete, the two hemispheres are transformed into a kind of cup or secondary optic vesicle. Its wall is formed of two laminæ: the internal one, representing the old distal hemisphere, will become the retina proper whilst the external one, originally the proximal hemisphere, will form the pigment epithelium lining the retina outside.

All the retina proper is derived from the internal membrane of the secondary optic vesicle. Beside the retina proper and its epithelium, the two membranes of the secondary optical vesicle also form the ciliary part and the iridic part of the retina.

This formation of the secondary optic vesicle by invagination of the proximal hemisphere of the primary vesicle enables us to understand the inversion of the retina. This term denotes the apparently abnormal situation of the sensory neuro-epithelium or layer of rods and cones at the anterior or inner surface of the retina. In all other sense-organs, the sensory epithelium is turned towards the exterior, or at least towards the medium which transmits the external stimulus to it. The retinal inversion is not a physical or a physiological necessity since there are non-inverted retinæ in the animal series. The inversion is an embryological necessity; we must bear in mind that only the ectodermic layer, the layer in relation to the external medium, is capable of giving rise to a sensory epithelium. Now, when the ectoderm of the embryo becomes invaginated at the dorsal line to form the primary nervous canal, the ectodermic surface thus invaginated becomes the internal surface of the canal. It is this surface, and only this, which has the property of producing sensory cells. The retina proper develops from the internal or distal membrane of the secondary optic vesicle; this membrane derives from the primitive ectodermic surface and it is this surface that is capable of producing the sensory epithelium of the retina. In other words, the

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visual cells occupy (in vertebrates) the posterior or outer retinal surface because this surface derives from the primitive ectodermic surface.

Embryology also gives us an explanation of the presence of neuroglia in the retina. The neuroglia (*neuros*, nerve; *glia*, glue) is a fine felt-work of extremely delicate fibres which, in the nervous centres, bind the nervous elements together. The fibres of the neuroglia are, in reality, processes from numberless minute cells; the body of each cell is extremely small and the processes extremely numerous. The processes of the neuroglia cells are wrapped closely round the nerve fibres of the white matter and since they thus form a support and a covering for the fibres, the latter no longer need their natural external covering; in other words, the nerve fibres of the white matter possess no neurilemma. In the same way, neuroglia forms the supporting base for the nervous constituents of the grey matter.

Recent researches (Ramon y Cajal) have shown that the neuroglia cells of the nervous centres are derived from the ependyma or lining membrane of the central canal of the spinal cord and of the cerebral cavities or ventricles. Therefore, neuroglia can only exist where there has been an ependyma, i.e., a central cavity or canal. Such is the case for the retina and optic nerve derived from the hollow peduncle of the primary optic vesicle. Thus we have another proof of the fact that the retina is not an independent organ, but an expansion of the nervous centres. In the retina the neuroglia cells become modified so as to form the long fibres we shall describe presently under the name of Müller's fibres. These fibres extend from the internal to the external limiting membrane and constitute the support for the nervous elements.

**Inversion of the Retina in Higher Animals.**

We have already pointed out that the inversion of the retina in man and in most vertebrate animals is not a physiological necessity. There are types of eyes (e.g., those of the higher molluscs) in which the retina is not inverted. It is developed in the form of a depression or fossa in the outside ectoderm; the anterior orifice of this depression may be simply narrowed and remains in communication with the medium (water) in which the animal lives, as is the case in the eye of the nautilus, or again, may be closed in such a way that it constitutes a vesicle under the transparent ectoderm; this occurs in the eyes of the higher molluscs (gasteropodes) in which there is a crystalline lens developed from the ectodermic envelope closing the ocular cavity.

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It is clear that in an eye of this type, entirely derived from the outer ectoderm, the retina cannot have the same structure as one of cerebral origin. In the first place, it only shows the sensory epithelium or rod-layer. The rods, which are due to a direct differentiation of superficial ectodermic cells, are directed forward: the retina is not inverted. Besides, what corresponds to the second and third neuron, i.e., to the cerebral part of the human retina, is entirely included in the optic lobe, which is a part of the brain. In an eye of this type, the fibres of the rods, united so as to form a kind of optic nerve, traverse a cartilaginous wall (scleral cartilage which may be compared to the orbital wall of vertebrates) and go, in arborescent fashion, into the optic lobe. In this lobe we find the bipolar cells so arranged as to establish a communication with the multipolar cells which may be regarded as corresponding to the ganglionic cells of the human eye.

**The Pineal Eye.**

In a previous chapter we have alluded to the pineal eye of some reptiles. The pineal eye results from the evolution of the epiphysis, a hollow pouch or sac which, in all vertebrate animals, proceeds from the roof of the middle part of the embryo brain. In birds and mammals, the epiphysis of the embryo becomes atrophied, the pineal gland being all that is left of it.

In some saurians, this pouch, very similar to a primary optic vesicle, increases in length and when it reaches the skin, is transformed into an eye by fairly simple modifications. The distal wall of the pouch thickens into a transparent crystalline lens. The proximal wall is transformed into a retina, the edge of which is consequently in continuity with the edge of the lens: the two organs, the functions of which are so different, have a same ectodermic origin. The peduncle of the pouch, originally hollow, becomes the optic nerve. The rods are on the anterior retinal surface, this surface corresponding to the internal surface of the cavities of the embryo brain. Though the retina of the pineal eye is of cerebral origin and is produced by a cerebral vesicle, it is not inverted because there has been invagination and no production of a secondary vesicle.

The pineal eye, in those species in which it still exists, is generally found in a state of arrested development and even when it is fairly well formed, as is the case in Hatteria, it does not serve a useful purpose. This supplementary eye was enormously developed in the great saurians of the Jurassic period, and there is no doubt that in these animals



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it constituted a most important organ, the necessity for which disappeared owing to the altered surrounding circumstances.

**Similarity of Embryological Origin of the Retina and the Crystalline Lens.**

The retina and the crystalline lens, although very different in appearance, present in some animal species a similarity of origin which is of great interest. This similarity of origin is very easy to understand since both the retina and the lens are ectodermic formations. It explains the fact, recently discovered, of the regeneration of the lens by the pars ciliaris retinæ in some amphibians. In the days following the extraction of the lens of a triton or of a salamander, the two laminæ of pigmented epithelium forming the pars ciliaris retinæ become the seat of a reaction characterised by a considerable thickening and by depigmentation, and after about fourteen days a new lens is formed.

**The Structure of the Retina in front of the Ora Serrata.**

A few words on the structures derived from the optic vesicle in front of the ora serrata may be useful. Though the retina ceases to exist as a nervous membrane in front of the ora, the two laminæ of the secondary optic vesicle are, however, represented up to the pupillary border where they become united: this continuation of the two laminæ of the secondary optic vesicle in front of the ora serrata constitutes the ciliary and the iridic parts of the retina. The external lamina, continuation of the pigment epithelium, conserves its character of a single layer, deeply pigmented. The internal lamina, continuation of the retina proper, but reduced to a single layer of cylindrical cells, is little or not pigmented up to the root of the iris. In the portion which corresponds to the folds of the ciliary processes it presents, as a special character, a longitudinal striation of its protoplasm, probably connected with the function it performs of secreting the aqueous fluid. From the root of the iris forwards, it becomes as loaded with pigment as the anterior lamina, so that the two form a continuous, completely black membrane, the cellular constitution of which can only be recognised in albinoes or in microscopic preparations artificially depigmented.

The special adaptations of the ciliary and iridic portions of the retina are not limited to the secretion of aqueous and to the opacification of the iris. The researches of Vialleton have proved, as we have explained before, that the dilator of the pupil is also derived from the pars iridica retinæ.

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## CHAPTER XIII.

### THE NERVOUS APPARATUS OF THE EYE—*(Continued)*. MICROSCOPIC STRUCTURE OF THE RETINA.

**History of the Subject.**

A brief history of the subject will show how the modern ideas on the constitution of the retina and visual centres, and on the working of the nervous apparatus of the eye generally, have been arrived at.

The assimilation of the retina to the cerebral substance is a very old notion mentioned in Galen's work (about 200 A.D.) but the retinal structure could not be studied without the microscope. All that the anatomists of the 17th and 18th centuries knew was what could be ascertained by the naked eye. Ruysch found that by maceration the retina could be divided into what he called a nervous layer, corresponding to the retina proper, and a limiting membrane, placed within the nervous part. Zinn, and after him Jacob (1819), observed that between the nervous layer and the choroid it was always possible, by maceration, to isolate a fine membrane which, at first, Jacob regarded as a serous membrane independent of the retina, but which he recognised later on as a part of the retina. We know now that this Jacob's membrane, easily separated in fishes' eyes, is formed by the juxtaposition of the rods and cones, separated from their fibres at the external limiting membrane. Thus, in the pre-microscope period, the retina was thought to be made of three layers: a limiting membrane, an intermediate membrane or retina proper, and Jacob's membrane.

Leuwenhoek (1722) observed the voluminous rods of the frog's retina by means of lenses manufactured by himself, but his discovery could not have any result at a period when the constitution of living tissues was not known. It was only after Bichat had created histology (1801) by introducing the notion of tissues, and after the microscope had become sufficiently perfected, that anatomists began to study the retina on a scientific basis.

Treviranius (1834) discovered again the rods and cones of Leuwenhoek; he regarded them as the ends of the optic nerve fibres, but, strangely enough, he thought they were at the internal retinal surface. It was about 1840 that histology was definitely erected as an exact science by the researches of Schwann, Henle, Remak and others, who

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proved that the cell is the fundamental element of all tissues. At this period, however, the only method of investigation was the dissociation of the constituents of the tissues, and it was still impossible to ascertain the exact relations of the various parts in such a complicated membrane as the retina. Henle recognised the layer of optic nerve fibres; Hanover discovered the ganglionic cells, which he assimilated to the cells of the nervous system. He had previously ascertained, on preparations of retinæ fixed and hardened in chromic acid, that the rods and cones were really in the external part of the retina.

Kolliker and H. Müller (1854) were the first to introduce staining in microscopic work, and to advance the opinion that the rods and cones were the perceiving retinal elements, all the other layers being merely conductors transmitting the stimulation produced by rays of light in the rods and cones. They regarded the mosaic arrangement of the rods and cones and their very minute diameter as eminently favourable for the perception of accurate visual sensations. A year later Müller gave another proof (still accepted in our days) of his assumption; he showed that the vascular figures of Purkinje are produced by the shadows of the retinal vessels on the percipient layer, and he demonstrated, by measurements on sections, that this layer can only be that of rods and cones.

The question that arose next was: How is the visual impression transmitted from the rods and cones to the optic nerve fibres? It was in answer to this question that the notion of the retinal fibre came to light. This notion has been very rich in results and it is still accepted, even now, though in a form very different from the original one. Kolliker and Müller thought that, although they had been unable to see it, a connection was bound to exist between the rods and cones and the fibres of the optic nerve. They were inclined to think that this connection was established through the radial fibres Müller had discovered in 1851; the fibre of Müller is not, however, the true retinal fibre, that is the connection between the percipient elements and the nervous centres. The error is easily understood when we consider the radial direction of Müller's fibres, and especially when we remember that the notion of two separate substances in the retina, namely, the nervous substance proper and the substance of support, had not yet been generally accepted.

Müller died in 1864 without having been able to ascertain what, in the retina, was nervous tissue and what was supporting tissue; he had advanced the theory of the retinal

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fibres, i.e., of a series of elements directed radially and connecting the rods and cones to the nervous centres, but he could not give a proof of the real existence of this connection. However, he had directed retinal histology in the right channel and had advanced hypotheses which, 50 years later, were justified by the researches of Ramon y Cajal (individual conductibility at the fovea; reduction between the perceiving and the conducting elements in other parts).

Max Schultze continued Müller's researches, and, in 1865, he published a most brilliant work on the subject. He described the exact arrangement of the rods and cones, their different distribution in diurnal and nocturnal animals, their different function, the histological structure of the macula, and he distinguished in a perfectly clear way the nervous elements from the supporting ones. His schematic diagram and his nomenclature of the retinal layers are still regarded as classical in our day.

In fact, prior to the recent methods of investigation, it was well understood that the rods and cones were the percipient elements, and the efforts of scientists were directed towards the discovery of what was regarded as an absolute physiologic necessity, namely, a substantial continuity between the rods and cones on one hand, and the optic nerve fibres on the other. The possibility of a nervous conductibility otherwise than by continuity was not dreamed of.

From 1875 to 1886, two methods of coloration of nervous elements had been invented, that of Golgi (1875), modified later on by Ramon y Cajal, and that of Ehrlich (1886). The first has considerably altered our views on the relation of nervous elements generally, and the second has especially served to confirm the results of the first.

The method of Golgi and Cajal has fulfilled a desideratum which had long been regarded as unattainable, that of staining a few cells only in a mass of nervous substance, in such a way that these cells are coloured in all their length and up to the extremity of their finest processes. "When a bit of brain or of spinal cord or of retina, hardened in bichromate of potash, is placed for 24 hours in a solution of silver nitrate, a red opaque precipitate of silver chromate is formed in a small number of the elements of the grey substance and this gives a very clear and accurate picture of the finest cellular expansions" (Cajal). This method showed what had never been seen before, namely the whole of a nervous cell up to the utmost extremity of its protoplasmic and cylinder-axial processes. It was Cajal who observed that these cellular processes end freely and are not anastomosed with those of other cells. He found that a nervous

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cell, with its system of processes is an individuality, a "neuron," and that nervous conductibility takes place, from cell to cell, or from neuron to neuron, by contiguity, i.e., by contact (as in electric apparatus) and not by continuity, as was thought before.

Müller, Schultze and the authors of the period immediately preceding the birth of the new methods of investigation could not solve the problem of the retina because they were unable to trace the continuity of the rod- and cone-fibres in the outer and inner molecular layers, the cellular processes being apparently lost in these plexiform structures.

The progress realised by Cajal consists mainly in a bold generalisation of a few facts, well observed by Golgi's method, and in the establishment of the law of reciprocal relations between the nervous elements. In fact, Cajal was able to take the nervous system to pieces, cell by cell, since he proved it to be made of independent elements with free terminations.

The work of Cajal on the histology of the nervous system (1892) is actually regarded as a sort of Gospel on the subject of nervous and retinal structure. His researches on the retina, following those on the structure of the nervous system, were not started with the preconceived idea of finding in it intercellular connections of the same nature as that he had discovered in the brain, but on the contrary, to find out whether the retinal connections were really of the same kind as those he had ascertained in the nervous centres. He tried to find, in the structure of the retina, the confirmation of general laws, instead of accepting these laws as being established, and of applying them to the retina. His conclusions, which have been received with great favour by most modern histologists, are of greater value on this account.

The authors who first gave a nomenclature of the retinal layers did not know the real nature of the anatomical elements constituting these layers and they denoted them by purely descriptive terms such as rods and cones, granular and molecular layers, which merely indicate the appearance and not the true nature of the retinal elements.

**Microscopic Structure of the Retina.**

The nomenclature of Müller and Schultze is still given in many modern text-books the authors of which pay, in this way, a tribute to the memory of these pioneers. We give below the list of the retinal layers according to the views of Müller and Schultze together with the more scientific list of Ramon y Cajal.

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According to Müller and Schultze, the retinal layers from outside inwards are: (See fig. 22.)

(1) Pigment epithelium.
(2) Layer of rods and cones.
(3) External limiting membrane.
(4) External or outer nuclear layer.
(5) External or outer molecular layer.
(6) Inner or internal nuclear layer.
(7) Inner or internal molecular layer.
(8) Ganglionic layer.
(9) Layer of optic nerve fibres.
(10) Internal limiting membrane.

The different retinal layers, according to Ramon y Cajal, are:

(1) Pigment epithelium.
(2) Layer of visual cells (rods and cones).
(3) Layer of bodies or grains of visual cells, corresponding to the outer nuclear layer of Müller.
(4) External plexiform layer, corresponding to the outer molecular layer.
(5) Layer of horizontal cells, occupying the outer part of the inner nuclear layer of Müller.
(6) Layer of bipolar cells, corresponding to the inner granular layer.
(7) Layer of amacrine cells, occupying the inner part of the inner nuclear layer.
(8) Internal plexiform layer (cerebral plexus), corresponding to the inner molecular layer.
(9) Ganglionic layer.
(10) Layer of optic nerve fibres.

The two limiting membranes are not mentioned in Cajal's list as they do not correspond to true retinal layers; they simply mark the ends of Müller's fibres which constitute the framework supporting the nervous retinal elements.

The two layers in Cajal's list which do not occur in Müller's are the layer of horizontal cells and the layer of amacrine cells. The former is made of flattened and star-shaped cells, the bodies of which occupy the outermost part of the inner nuclear layer whilst their greatly ramified processes extend into and end in the outer molecular layer. The layer of amacrine cells or spongioblasts is placed in the inner part of the inner nuclear layer. As the name "amacrine" implies (*a*, privative; *macros*, long; *inos*, fibres) it has not

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been possible to demonstrate the existence of an axis-cylinder in these cells (which are nevertheless regarded by Cajal as true nerve cells) but they possess numerous extensively ramified protoplasmic processes which form a horizontal arborisation in the several strata of the inner nuclear layer.

The main structure of the retina is fairly uniform though the foveal or macular region differs to a slight extent from the rest of the membrane.

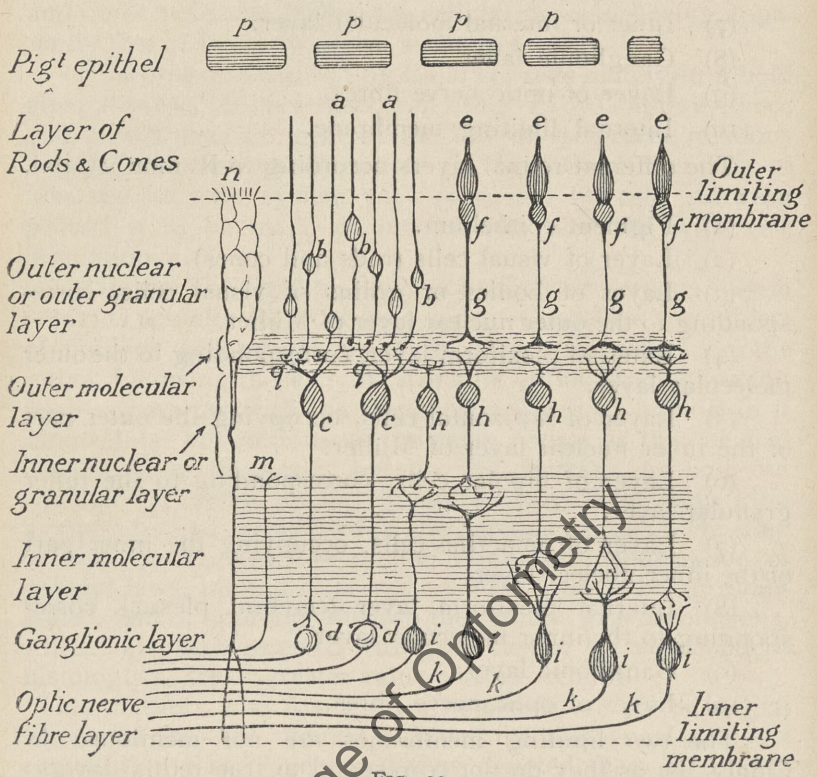


FIG. 22.

FIG. 22. SCHEMATIC APPEARANCE OF A SECTION OF THE RETINA PREPARED BY THE GOLGI AND CAJAL METHOD, SHOWING THE VARIOUS RETINAL LAYERS AND THEIR INTERCONNECTIONS.

*p p* are the hexagonal cells of the pigment epithelium layer. From their inner surface, protoplasmic filaments (not shown on the diagram) pass inwards between the outer segments of the rods and cones.

*a a*, rods with their fibres on the path of which the rod-granules or rod-corpuscles *b b* are placed. Each rod-fibre ends in a terminal knob; *q q* are the synapses by which the terminal knobs of the rods are connected physiologically, though not by continuity of matter, with the outer or dendritic processes of the bipolar cells *c c*. The inner processes or cylinder-axes of the bipolar cells end in fine branches surrounding (though not in direct continuity with) the bodies of the rod ganglionic cells *d d*.

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*e e* are cones with their cellular bodies or cone-granules or cone-corpuscles *f f* immediately below the inner segments of the cones and level with the outer limiting membrane. Each of the cone-fibres *g g* terminates as a cone-foot in the outer molecular layer. Each of the cone bipolar cells *h h* is articulated, i.e., forms synapses with a cone-foot, on one hand (by its outer dendritic processes), and with the outer dendritic processes of a cone ganglionic cell *i i* on the other hand. The latter articulations or synapses occur at different levels in the inner molecular layer.

The axons or cylinder-axes of both rod and cone ganglionic cells are continued into optic nerve fibres *k k*.

*m* represents one of the centrifugal fibres of the optic nerve proceeding from the nerve centres of the cerebral cortex and passing on with the true optic nerve fibres to end in the inner molecular layer.

*n* represents one of the supporting Müller's fibres forming the framework of the retina, the portion of that membrane which holds the nervous conductors in their position. The inner and outer ends of these fibres form the so-called inner and outer limiting membranes, shown in dotted lines.

The pigment epithelium layer, the bacillary layer or layer of rods and cones, the outer molecular layer, constitute together the first visual neuron, entirely retinal and nourished by osmosis through the chorio-capillaris layer of the choroid.

The layer of bipolar cells, or inner nuclear, or inner granular layer and the inner molecular layer constitute the second or intermediate visual neuron, entirely retinal and nourished by the capillary vessels of the retina.

The ganglionic cell layer and the layer of optic nerve fibres form the third visual neuron, partly retinal, partly orbital and partly cerebral, which is nourished by the retinal and cerebral blood-vessels.

The retina is, as we know, the sensitive ocular membrane, the sclerotic forming the skeleton and the choroid the nutritive membrane. The whole of the retina is not sensitive to light, the really sensitive part being made of the rods and cones or visual cells and of the cellular bodies attached thereto. This sensitive part constitutes the first visual neuron. Outside this is the pigment epithelium, which separates the rest of the retina from the choroid, and inside are the other retinal layers constituting the transmission apparatus.

A brief description of the various retinal layers will be found useful.

**Pigment Epithelium.**

In the embryo the pigment epithelium, which lines the retina outside and represents the proximal lamina of the secondary optic vesicle, is made of several layers of cells, but in the adult it is reduced to a single layer of very regular hexagonal cells extending from the edge of the papilla to the free pupillary border. Just now, we will study it as far as the ora serrata. In the human retina, the cells of the pigment epithelium are of almost regular hexagonal shape, this resulting from an equal compression in all directions. Their diameter varies from 12 to 18 microns, the smaller ones being found in the macular area.

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If we examine under the microscope the brown membrane formed by the exact juxtaposition of these cells the latter appear as if they were separated from each other by fine clear lines formed of a colourless intercellular substance (neuro-keratine); the collection of these lines constitutes a regular polygonal pattern, the reticular formation of Boll.

Viewed laterally, each cell appears as prismatic hexagonal, the superior part is not pigmented and contains a nucleus and small droplets of fat; the inferior part is loaded with pigment granulations and sends, between the rods and cones, protoplasmic filaments, also pigmented, which resemble the hairs of a brush. As already stated, these filaments lengthen under the action of light and retract in the dark. This fact, discovered by Boll, explains why a retina which has been illuminated is not so easily separated from the choroid as one which has been kept in the dark. The researches of Angeluci and Renaut have shown that during the action of light there is not only an increase in the length of the filaments extending from the inner surfaces of the cells of the hexagonal epithelium, but also a migration of the pigment from the bodies of the cells along the filaments themselves. It seems that under the influence of light the particles of pigment are propelled along the filaments so as to envelop the external segment of each rod or cone in a sort of pigmentary sheath. In the dark, not only do the filaments themselves retract, but the pigment which had been accumulated in them during the action of light moves back and returns to the bodies of the cells. This is evidently a process the purpose of which is to protect the percipient retinal elements against the action of a strong light.

The filaments of the pigment epithelium cells are much more developed in fishes, amphibia, reptiles and birds than in the human eye. According to Schultze, they exist in albino eyes and in the portion corresponding to the tapetum of mammals (in which the retinal epithelium is poor in pigment) but then they are deprived, either absolutely or relatively, of pigmentary grains. The pigmentary granulations contained in the base of the hexagonal cells and in the processes or filaments of these cells have, in the human eye, a spherical shape and are 1 to 5 microns in diameter. Kuhne has isolated the retinal pigment (fuchsine) and has found it different from the choroidal pigment or melanine. The former is hardly affected by chemical reagents but when removed from the cells of the epithelium it is very sensitive to the action of light which destroys its coloration. It is not probable that light produces a similar discoloration in the pigment of the living retina. The oil droplets contained in

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the non-pigmented part of the hexagonal cells seem to be more abundant in nocturnal animals (owl) than in man.

**Sensitive Part of the Retina.**

The sensitive part of the retina is made of two separate layers: the most external one is that of the rods and cones, the other is the outer nuclear layer. Between the two is the so-called external or outer limiting membrane which is not really a retinal layer but simply marks the position of the external ends of the fibres (Müller's fibres) forming the supporting tissue of the retina. In fact, the two layers (or the three if we include the limiting membrane) are composed of a collection of single neurons, the first visual neurons, the cellular parts of which (i.e., the rod- or the cone-granules) are most internal and the rods and cones (i.e., protoplasmic processes differentiated for a sensorial function of the greatest importance), form the most external part.

In most retinæ, the sensory epithelium is made of two varieties of cells placed side by side and characterised as visual cells by the presence at their free poles (which are turned toward the pigment epithelium) of special protoplasmic processes, more or less filiform and apt to receive the shock of the luminous vibrations on their points. The two varieties of visual cells are the rod-cells and the cone-cells (fig. 23).

Each visual cell includes: (1) a rod or a cone; (2) a fibre, which is thick in the case of a cone and thin in the case of a rod. On the path of the fibre, we find a cellular body (cone-granule or rod-granule) from which the cylinder-axis emerges to end freely in the outer molecular layer or external plexiform layer. The limit between the rod and cone proper and the rest of the visual cell is exactly marked by the external limiting membrane, and it is the part external to that membrane which is described as the layer of rods and cones.

The rods are thin, elongated structures, the dimensions of which vary in different species. They are made of two segments: the external one is vitreous in appearance and of geometric form; the internal is of protoplasmic nature and its form depends on the lateral pressure of the neighbouring elements. In man, the total length of the rods varies in different parts. It is about 60 microns near the posterior pole and diminishes gradually to 40 microns at the ora serrata. The thickness of the external segment is 1.5 to 2 microns.

The cones are shorter except at the fovea where they become more or less rod-like. Their length is about 25 to 30 microns. They are thicker at the inner end or base (6 microns) and are terminated externally by a finer tapering

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portion. Both rods and cones are closely set in a palisade-like manner over the whole extent of the retina between the internal limiting membrane and the pigment epithelium.

The rods and cones, though differing in size and shape, agree in many points of structure. Thus each consists of two distinct segments, an inner one and an outer one, the division between the two occurring, in the case of the rods, about the middle of their length (in man); in the case of the cones, at the junction of the finer tapering end-piece with the broader basal part. It follows that whilst the inner and outer segments of the rods are practically similar in shape and size, the inner one being, however, slightly bulged, the inner segment of a cone far exceeds the outer one in size, the latter (outer segment) appearing merely as an appendage of the inner segment.

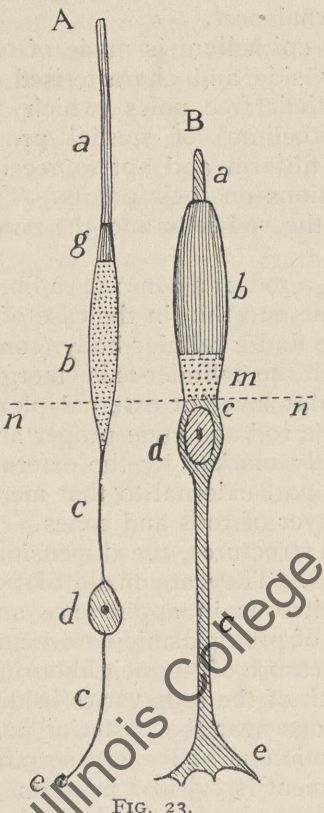


FIG. 23.

FIG. 23. VISUAL CELLS OF THE HUMAN RETINA. (Diagrammatic view; magnification about 1,000 diameters) (after Greef).

A. Rod-cell. *a*, external or outer segment of a rod, transparent, and appearing as if made up of piled up discs; it does not readily take vegetal or animal stains like hematoxylin or carmine and is not, therefore, of protoplasmic nature. *b*, Internal or inner segment of the same rod; it is transparent during life and becomes granular after death; it is of protoplasmic nature, as shown by the fact that it is stained pink by carmine.

Between *a* and *b*, we find what is called by Ranvier the intercalar body *g*; *c c* represent the rod-fibre, thin and occasionally varicose, with its terminal knob *e*. On the path of the rod-fibre is the cellular body *d* of the rod-cell (or rod-granule or rod-corpuscle) with its nucleus.

B. Cone-cell. *a* and *b* outer and inner segments of a cone corresponding to the similar parts of the rod-cell; they are variations of a same typical element. The cones are generally shorter and their inner segment is thicker than that of a rod except in amphibians in which the rods are enormously developed. The structure of the outer segment *a* of a cone is similar to that of the corresponding part of a rod. At the base of the inner segment *b* of a cone is what is called the myoid *m* which plays a part in the contraction of the cone; *c c* is the cone-fibre thicker than the rod-fibre; *e* is the terminal cone-foot. In the case of a cone-fibre, the cellular body or cone-granule or cone-corpuscle *d* (with its nucleus) is immediately below the end of the inner segment; the line *n n* represents the outer limiting membrane.

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The two segments of both rods and cones exhibit marked differences in their chemical and optical properties as well as in their structural appearance. In both rods and cones, the outer segment is doubly refracting while the inner one is singly refracting. Most stains (carmine, iodine, etc.) are taken by the inner segment but the outer segment is not coloured by these reagents. It is, however, stained greenish-brown by osmic acid.

The outer segment in both rods and cones shows a tendency to break up into a number of minute superimposed discs. It does so in a series of liquids such as aqueous fluid, artificial serum and especially in a 10% solution of sodium chloride. This evidently shows that the outer segment of the rod or the cone is made of a pile of discs which, in the fresh state, are united by a cement-like substance. It is curious to observe that whilst the outer segment is highly transparent laterally (in the fresh state), it forms, along its axis, a kind of reflecting surface, the purpose of which is perhaps to stop the luminous vibrations and to transform them into visual nervous impulses.

Beside the transversal striation already mentioned, a powerful microscope shows fine longitudinal markings or grooves on the outer segments of the rods. The ends of the outer segments of the rods are rounded and project into the pigment epithelium. The purplish-red colour of the retina resides entirely in the outer segments of the rods. A few rods are, however, of green colour, at least in some animal species.

The outer segments of the cones taper gradually to a blunt point; they do not show the longitudinal grooves observed in the corresponding parts of the rods but the transversal markings are even more evident. There is a delicate covering of neuro-keratine investing the outer segments of both the rods and cones, and this is more pronounced in the cones, so that the post-mortem separation into discs does not take place so readily in the cones as in the rods.

**Visual Purple.**

The external segments of the rods often show a red or green coloration though some rods are colourless. Boll, having observed that the retina is red in animals kept in the dark, found that this coloration is restricted to the external segments of the rods, and that it is never present in the cones. This property of the retina, to become red in the dark and to be discoloured in the light, belongs to the lamellar substance of the outer segments of the rods: it follows that

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the red colour will be more marked in retinæ rich in rods and will not occur in retinæ which are rodless, like those of most reptiles.

As far back as 1866, long before the discovery of the visual purple, Kuhne had observed: (1) that the retina of diurnal birds is rich in cones, whereas that of nocturnal birds contains a greater proportion of rods; (2) that the more nocturnal the habits of an animal are, the longer the external segments of the rods in its retina; (3) that there are, in the retinæ of diurnal birds, drops or droplets of a fatty substance, strongly coloured, and occurring exclusively in the cones, and that the similar drops in nocturnal birds are colourless or at least pale yellow.

Kuhne had also observed the red colour of the rods of the owl but he did not understand the value of the fact at the time. When the discovery of Boll was published, Kuhne immediately thought there must be some antagonism between the presence of the purple which is destroyed by light and that of the fatty drops with a fixed coloration. He came to the conclusion that the latter constituted a means of permanent absorption of coloured light. He saw that the retina of the hen and the pigeon, very rich in coloured drops, does not show any trace of purple, whereas a fine red colour, fading in the light, is found in the retina of the owl.

To sum up, nocturnal, or rather, crepuscular vertebrates (owl, rat, etc.) possess a very abundant purple. Animals of exclusively diurnal habits, as the hen and those birds which take shelter as soon as the crepuscule occurs, have no purple at all. This is also the case for reptiles, most of which are only active in the sun; nocturnal reptiles, the gecko for instance, have rods only in their retinæ and therefore have visual purple. Those animals which, though chiefly diurnal, are not deprived of crepuscular vision (and this is the case for man) possess retinal purple but not in such abundance as true nocturnal beings.

Though absence of purple is a proof of exclusively diurnal vision, this absence of purple does not necessarily imply that of rods. There are rods which do not exhibit any purple; the retina of the hen or the pigeon does not show any coloration after a long stay in the dark; yet it possesses a certain number of rods which, therefore, must be deprived of purple: the fact has been verified by microscopical examination of such retinæ in the fresh state; the rods were found absolutely colourless.

The retinæ of the various kinds of bats also show purpleless rods but it must be observed that these animals are all

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microphthalmic; their eyes are in a state of arrested development and the destruction of these organs does not prevent the animal from moving about in perfect security. It is not astonishing, therefore, to find that the purple is absent since the visual function only exists in a rudimentary form.

In the human eye, the purple is absent in a retinal zone of 3 to 4 mms. behind the ora serrata, and of course in the fovea which is made of cones only.

These considerations show that the visual purple does not play an essential part in all circumstances, but that it is necessary for nocturnal vision. The purple renders the eye more sensitive to low illumination, and the organs which contain it, the external segments of the rods, are the organs of vision in low illumination. According to Parinaud, acquired hemeralopia is caused by an arrest in the production of purple.

The visual purple seems to be secreted by the pigment epithelium since it has been found by Kuhne that on the part corresponding to an artificial detachment in the frog the purple is still regenerated. The experiment is even successful on a frog's eye freshly enucleated: the regeneration of purple goes on for a time. If, however, a solid body is introduced between the retina proper and the pigment epithelium, the rods remain colourless in the dark. How the purple is produced by the epithelium is not known. The pigment has evidently nothing to do in the matter since the purple is found in the retina of albinoes and in the portion of the retina of carnivorous animals corresponding to the tapetum, i.e., in a region in which the epithelium is very poor in pigment, if not absolutely deprived of it.

Amongst the purple coloured rods of the frog's retina, Boll has observed rods of a green shade which are discoloured by light, though more slowly than the purple ones. Some authors think that the green colour does not really exist and is but an effect of contrast with the red colour of the surrounding part: the so-called green rods would, according to them, be colourless. The matter is not elucidated.

In diurnal birds, many reptiles and some amphibians, some of the cones contain bodies or drops of an oily appearance variously coloured in red, yellow, green and even blue. These bodies are absent in mammals and in man; they are also absent in fishes, except the sturgeon. Nocturnal birds, with few cones, show only a small number of these bodies, coloured pale yellow. The coloured body occurs in the inner segment, near the junction with the outer one. It occupies the whole diameter of the segment, so that light must necessarily pass through it. All cones are not provided with

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coloured bodies. The colour of these bodies is not modified by light: in fact the presence of coloured bodies is, to a great extent, antagonistic to that of the purple: the coloured bodies predominate in animals of purely diurnal habits while they are absent or little developed in crepuscular beings.

**Contractility of Retinal Cones.**

Van Genderen Stort found that the cones contract under the action of light and retract in the dark. It is the protoplasmic part of the internal segment or more exactly the portion of the outer segment that rests on the outer limiting membrane which contracts and retracts. For this reason, this portion is called the myoid of the cone. There seem to be contractile and non-contractile cones. This contractility to light, in an element adapted to luminous perception, may exist in other anatomical elements. In any case, it is not an essential condition for vision since it takes time to occur.

**Repartition of Rods and Cones in the Retina.**

The repartition of the rods and cones in the human retina is of interest. On a fresh retina, examined by its external surface or, better still, on Jacob's membrane isolated by maceration, the rods appear in the form of small circles, the cones as darker and larger circles, owing to the larger diameter of the internal segment. It is, therefore, possible to ascertain the relative distribution of these elements. At the fovea and within an area of 0.5 to 0.8 mms. round it, there are cones only, a few rods appearing at the periphery of the minuscule region considered. (The subject will be taken again in the study of the foveal part.) In the immediate neighbourhood of the above area, each cone is surrounded by a row of rods, but beyond this, and not farther than 1.2 to 1.5 mms. from the foveal centre, the cones become more distant and separated from each other by two to four rows of rods. The proportion of rods increases up to the neighbourhood of the ora serrata; then, the number of rods diminishes abruptly, that of the cones remaining the same: hence the existence of lacunæ between the cones. According to Krause, there are 130 million rods and 7 million cones in the human retina.

The proportion of rods and cones in animals is not a generic character but a character of adaptation. It varies with the habits of life, with visual adaptation (diurnal, mixed or nocturnal) and not with the zoological class or order of the animal.

Amongst fishes, some are very rich in cones, some in rods: there must be, of course, a great difference between

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fishes living near the surface and those living in depths in which very little light can penetrate. Diurnal birds have more cones than rods whereas in nocturnal ones, the rods predominate.

In fact, it seems well established that the rods predominate and increase in length in animals with nocturnal vision. In diurnal animals, the cones become abundantly intermixed with the rods and in diurnals deprived of crepuscular vision, they predominate or even exist by themselves, without any rods. The conclusion is that the rods are the elements capable of adapting themselves to crepuscular vision by the presence of the purple, whereas such an adaptation is impossible in the case of the cones which can only perceive high degrees of illumination. We must not conclude, however, that the rods cannot serve to diurnal vision: many night birds, when adapted, see very well in daylight; we do not know, it is true, to what extent they can see colours.

The law of Schultze, completed by the law of Kuhne, sums up the matter. In the retinæ of nocturnal animals the rods predominate and assume an unusual length (Schultze). The visual purple is developed in proportion to the development of crepuscular vision; it is entirely absent in animals deprived of crepuscular vision (Kuhne).

The so-called external limiting membrane, as we have already pointed out, is formed by the terminal spreading of Müller's fibres. We only mention it from the topographic point of view, as it is not a continuous membrane. On sections it appears as a thin transversal line on which the inner segments of the rods and cones rest by their bases; it separates them from the rest of the visual cells.

**Outer Nuclear or Outer Granular Layer.**

The principal elements of this layer differ in the case of the cone-cells and in that of the rod-cells. The bodies or granules of the rod-cells (rod-granules) are, in most parts of the retina, more numerous than the cone-granules. They can be regarded as enlargements or swellings in the course of delicate fibres which extend from the inner ends of the rods (at the external limiting membrane) through the thickness of the layer, to the outer molecular layer or plexiform layer. The body or granule of each rod is situated at a different part of the course of the corresponding fibre, so that on a section, the rod-granules appear to occupy the whole thickness of the layer. A rod-granule never rests on the outer surface of the molecular layer, so that there is always a more or less long segment of fibres between the rod-granules and the molecular layer.



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Each rod-granule shows, in the fresh condition, a remarkable cross striped appearance, the strongly refracting substance which mainly composes the granule being interrupted by bands of clear, less refracting material. Each rod-fibre is continuous at the outer end with one of the rods, and at the inner end it terminates in the superior strata of the outer molecular layer, by a knob, in the case of mammals, nocturnal birds and fishes, or in a small protoplasmic mass from which fine fibrils end freely in the molecular layer in the case of amphibians, reptiles and diurnal birds.

The cone-granules (fewer in number than the rod-granules) are distinguished from the latter by the absence of striation and by the fact that (except at the fovea, as we shall see presently) they occupy the part of the outer nuclear layer nearest to the external limiting membrane. The cone-fibre is much thicker than the rod-fibre and its extremity rests on the surface of the outer molecular layer by a somewhat pyramidal base termed the cone-foot.

As already mentioned, the first visual neuron is formed of the sensorial epithelium, i.e., of the rods and cones with their fibres and granules or bodies. This neuron is not vascularised but is nourished by diffusion of nutritive plasma derived from the chorio-capillaris layer of the choroid. In other words, the choroid nourishes by osmosis the pigment-epithelium and the external part of the retina.

**The Outer Molecular Layer or External Plexiform Layer.**

This is a tenuous layer, fibrillar in appearance, generally free from cellular elements and in which the ordinary methods of coloration show that the terminal knobs of the rods and the feet of the cones, on the one hand, and the outer processes of the bipolar cells, on the other, are lost. The method of Golgi has enabled Cajal to ascertain that the outer molecular layer is the zone of articulation of the feet of the visual cells (terminal knobs of rods and cone-feet) with the outer protoplasmic arborisations of the bipolar cells. In the external part of the layer, the terminal knobs of the rod-fibres are surrounded by the fine ramifications of the outer processes of the rod-bipolar cells. In the internal part, the cone-feet spread in front of flattened arborisations of the cone-bipolar cells. Müller's fibres form the support of the elements of this layer by means of finely ramified fibrillæ.

**Inner Granular Layer.**

The term is used here in its topographic sense to denote the layer formed by the bipolar cells, the horizontal cells and the amacrine cells

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The bipolar cells are the most numerous and the most important elements of the layer. Each cell possesses two processes, generally extending radially (occasionally obliquely, as in the case of some reptiles) from the outer to the inner molecular layer. In mammals, Cajal describes three kinds of bipolar cells: (1) the rod-bipolar cell with outer arborisation articulated with the terminal knob of a rod; (2) the cone-bipolar cell, the outer arborisation of which is flattened and articulated with a cone-foot; (3) the giant bipolar cell with a greatly extended terminal arborisation probably also connected with a cone.

The bodies of the rod-bipolar cells may occupy any position within the layer; their outer processes, very fine and very numerous, spring from a single trunk or from separate ones and within the angles formed by their terminal arborisations, a various number of rod-knobs are placed (15 to 20 for large cells; 3 to 4 for small ones).

The bodies of the cone-bipolar cells are almost always near the outer molecular layer; their flattened ascending arborisations extend on a much larger horizontal surface than those of the previous kind of cells and form a thick plexus immediately in front of the feet of the cone-fibres.

The giant bipolar cells answer fairly well to the same description as that of a cone-bipolar cell except that their bodies are of larger size and that the arborisations from the outer pole also extend on a larger surface. These cells seem to be chiefly connected with cones.

In the three kinds of bipolar cells, the processes from the inner pole are similar; they branch into fine arborisations which penetrate into the inner molecular layer where they become articulated with the outer or dendritic processes of the ganglionic cells.

From the brief description just given, it appears that the bipolar cells are elements of reduction inasmuch as they transmit to a single ganglionic cell the impressions received by a number of rods or cones (except at the fovea, as we shall see presently).

The layer described by Cajal as layer of horizontal cells occupies the outer part of the inner granular layer. The chief elements are star-shaped cells, the axons of which are directed towards the outer molecular layer where they end round the terminal knobs of the rods. The descending dendritic processes, highly arborised, are lost in the inner molecular layer. The purpose of these cells is not fully elucidated. As we shall see presently these cells seem to connect the rods and cones.

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Another layer described by Cajal, which is also a part of the inner nuclear layer of Müller and Schultze, is the layer of amacrine cells (cells without a cylinder-axis or axon: unipolar cells of Ranvier). These cells are more voluminous, as a rule, than the bipolar cells; they are coloured more strongly with carmine or hematoxylin. They form a row (a special layer according to Cajal) just in contact with the inner molecular layer into which their inner processes pass and articulate with the outer processes of the ganglionic cells. The purpose of these cells is not completely elucidated.

**Inner Molecular Layer or Inner Plexiform Layer.**

With the ordinary methods of fixation (bichromate of potash; osmic acid) this layer appears as finely granular and, with high powers, it looks like a felt-work without cellular elements. The researches of Cajal have made it clear that it forms the zone of articulation of the bipolar cells and amacrine cells on one hand and the ganglionic cells on the other.

**Ganglionic Cell Layer or Layer of Multipolar Cells.**

The chief elements of this layer are the ganglionic cells or cells of origin of the optic nerve fibres. It also contains spider-cells of neurogliar nature and disseminated amacrine cells. These elements are kept in their proper relations by Müller's fibres which are very apparent at this level. The layer thus formed is placed between the inner molecular layer and that of the optic nerve fibres. The latter is very thin near the ora serrata, so that the ganglionic cells almost touch the internal limiting membrane in that part; it becomes thicker towards the papilla. The ganglionic cells form a single row in which they are exactly juxtaposed in the central part of the fundus and become more and more distant from each other as the ora serrata is approached. Towards the edge of the fovea, the cells are gradually massed so as to form as many as 6 to 10 superimposed strata on the projecting border of the foveal pit; the reason for this arrangement will be made clear when we study the retinal structure in the macular area.

The size of the ganglionic cells varies in man from 10 to 30 microns. The smallest are found near the fovea; the largest near the ora serrata. The ganglionic cells are typical multipolar cells similar to those found in the grey matter of the nervous centres; their dendritic processes are arborised in the inner plexiform or molecular layer where they articulate with the inner processes of the bipolar cells; their cylinder-axis processes, which are never ramified, are connected with the optic nerve fibres.

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**Optic Nerve Fibre Layer.**

This layer is essentially made of the cylinder-axis processes of the ganglionic cells. These processes, coming from every point of the retina, converge toward the papilla, forming themselves into more and more voluminous bundles. These bundles are supported by the feet of Müller's fibres and by neurogliar spider-cells. The bundles of fibres are thin at the periphery and increase in size towards the papilla by the addition of new fibres coming from the subjacent ganglionic cells.

The fibres born of the macular ganglionic cells form two separate systems: (a) a fine loose bundle at the bottom of the foveal depression and extending in straight lines towards the papilla; (b) a kind of perimacular ring from which two arched bundles, one above, the other below the fovea, are also directed towards the papilla. Thus the whole of the fibres proceeding from the macular area constitute a sort of fan-shaped radiation, the apex of which is at the papilla; these fibres constitute what is termed the papillo-macular bundle. The bundles from the rest of the retina are all converging towards the papilla. The fibres which reach the nasal side of the papilla have an exactly radial direction; those which reach the temporal side arch round the papillo-macular bundle, forming curves concentric to the macula. Those in the neighbourhood of the horizontal meridian are at first directed towards the macular, but as they reach a point 3 to 4 mms. from the macular edge, they turn above and below the papillo-macular bundle.

The fibres which form the various bundles of the optic nerve fibre layer originate, as stated just now, from the axons of the ganglionic cells and are, like these cells themselves, of different sizes; some are of extremely, almost incommensurable, minuteness; some, the stoutest, have a diameter of 3 to 5 microns.

In man and most vertebrates, the fibres remain naked and reduced to their axis-cylinders in the retina and the papilla. It is only at the posterior surface of the lamina cribosa that they simultaneously acquire their myeline sheaths. In the rabbit and the goat, some of the retinal fibres have a myeline sheath and the appearance, with the ophthalmoscope, is that of a transversal, white, brilliant patch on either side of the disc. A similar appearance is observed occasionally in the human fundus as an abnormality of development.

The so-called internal or inner limiting membrane appears on sections as a fine line separating the retina from the vitreous. It really belongs to the retina and is independent

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from the hyaloid, on which it is simply applied. It is not difficult to inject a liquid between the two, and many reagents permit an easy separation of the two membranes.

Though the limiting membrane appears continuous and homogeneous on a section it is not, however, an isolable membrane. It is simply the mosaic formed by the exact juxtaposition of the feet of Müller's fibres. It follows that the membrane does not really exist, any more than the external or outer limiting membrane. If the retina is impregnated with a 3% solution of silver nitrate, the vitreous and the hyaloid being carefully removed, and is placed, internal surface upwards on a slide, the limiting surface appears as a pavement of polygonal elements, separated by black lines, the polygons being formed by the broad feet of Müller's supporting fibres, cemented by an intercellular substance similar to that found in endothelium. The limiting membrane is absent in the part corresponding to the papilla, a region in which Müller's fibres do not exist.

**Müller's Fibres.**

Müller's fibres, forming the framework of the retina, resemble the long neurogliar cells, which, in the embryo of vertebrates extend through the whole of the nervous centres, from the ependyme or central cavity to the external surface. Müller's fibres may be regarded as a modified form of neuroglia.

They consist (see fig. 22) of long cells directed perpendicularly from one limiting membrane to the other, like pillars connecting the floor of a room to the ceiling. They begin at the inner surface of the retina by a broad conical foot or base which may be forked; the bases of adjoining fibres are united together at their edges so as to give, in vertical sections of the retina, the appearance of a boundary line, termed the internal limiting membrane.

The Müllerian fibres pass through the layer of optic nerve fibres and the ganglionic layer, either with a smooth contour, or with two or three well marked lateral projections. Diminishing in size, they pass through the inner molecular layer and the inner granular or nuclear layer. In the latter, each fibre is characterised by the presence of a clear, oval nucleus situated on the side of, and in close adherence to, the fibre to which it belongs. On reaching the outer nuclear layer, after having passed through the outer molecular layer, the fibres break up into fibrils and thin lamellæ, and in this form they pass outwards through the layer, between the granules and the rod- and cone-fibres, enclosing these structures and forming partial sheaths for them. At

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the level of the bases of the rods and cones the numerous offsets terminate abruptly along a definite line which marks the boundary between the outer nuclear layer and the layer of rods and cones, which has been termed the outer or external limiting membrane.

The above description shows that neither the outer nor the inner limiting membrane is a continuous, isolable layer: in fact, some of the finer fibrillar offsets of the Müller's fibres pass a short distance beyond the so-called outer limiting membrane and closely invest the bases of the inner segments of the rods and cones.

According to Cajal, not only do Müller's fibres serve to form the support of the nervous elements of the retina, but they also play a similar part to that of the insulating material in an electrical apparatus: they prevent the diffusion of the current of nervous impulses.

**Special Structure of the Macular Area.**

We have said just now that the structure of the retinal macular area, though similar in many respects to that of the rest of the retina, yet differs in a way which is calculated to improve the working condition of this most important region. In most text-books, the term fovea applies to the minute punctiform depression at the centre of the yellow spot or macula lutea. This pit was at first thought to be a real hole (foramen centrale) and later on, to be a blind hole (foramen cœcum). There is now a tendency to modify this nomenclature which, however, is still frequently used.

A careful microscopic examination of a section of the retina shows that the central depression is not localised to the old fovea: the latter forms merely the bottom of a more extended depression with a slightly projecting edge. This concave and shallow depression, oval in shape, measures on an average 1.7 mms. along its long axis (horizontal). On the other hand, Müller had found that the transversal diameter of the yellow spot or macula lutea was about 2 mms. It follows that the yellow colour is present in the whole of the concave depression and perhaps a little beyond it. The term fovea, applied to the whole of the concave depression, is preferable to that of macula lutea since the coloration is only visible on a retina examined flat; beside, it is a more general term since it applies to a constant configuration, resulting from special histologic modifications.

Therefore, in what follows, the term "fovea" will be used to denote the whole of the central fossa of the retina, the part which corresponds to the oval surface, seen surrounded by a bright ring when a young subject is examined

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with the ophthalmoscope. Thus defined, the fovea is a slight depression the edge of which slightly projects on the surrounding retina. It has a concave surface and a central depression, the bottom of which, termed the fundus of the fovea (fundus foveæ), corresponds to the old foramen cœcum or to the fovea in the strict sense of the term. Measurements taken by Dimmer on good sections have shown that the diameter of the fovea varies from 1.4 to 2 mms. the average value being 1.7 mms. The diameter of the fundus foveæ is 0.2 to 0.4 mms. At the bottom of the fovea, the retina is thinner than elsewhere and only measures from 75 to 120 microns in thickness. On the edge, there is a greater thickening on the nasal than on the temporal side: (275 to 410 microns on the nasal side and 220 to 350 on the temporal side). Schultze and Krause, who were amongst the first to study the retina systematically, described the foveal border as more projecting than it really is. They used defective methods of fixation and, owing to this, the fovea apparently gained in thickness at the expense of its area. More recent researches, on retinæ well fixed by vapours of osmic acid, have shown that the border of the fovea is really little projecting, and that the feeble concavity of the surface exactly corresponds to the ophthalmoscopic reflexes.

The ophthalmoscope and the examination of the retina with the naked eye or with a magnifying glass show that the pigment epithelium is particularly dark on the part corresponding to the fovea. There the hexagonal cells are smaller (12 instead of 16 to 18 microns) and more deeply pigmented than in the rest of the layer. Their protoplasmic filaments penetrate also more deeply between the foveal cones than between the cones and rods in the rest of the retina.

A microscopic examination shows that the proportion of cones increases towards the fovea, that this increase continues within the foveal area and that, in the central part, there are cones only and no rods. The foveal cones differ from those of the rest of the retina: they are thinner and so much more compressed together that they become hexagonal. It follows that a greater number of cone-ends occurs in the unit of area of the fovea than in any other retinal region. According to Schultze, this modification occurs in a small region (200 microns in diameter) round the centre of the fovea. This fact agrees fairly well with Dimmer's measurement of the fundus foveæ (0.4 to 0.2 mms.) Whilst they become thinner, the foveal cones also become longer. The fact that the foveal cones are thinner and more closely packed than those of the rest of the retina explains the higher acuity of this part of the fundus.

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The other retinal layers all diminish in thickness at the fovea or, more exactly, they are rejected obliquely towards the periphery, so that, at the bottom of the foveal depression, there is little more than the first visual neuron, that is the layer of cones and the outer granular layer.

It must be observed that the ganglionic layer undergoes striking changes in the foveal region. Whereas it is made of a single row of cells in the rest of the retina, it becomes thicker at the projecting edge of the fovea and contains from 6 to 10 strata of superimposed cells. This increase in the number of ganglionic cells had been observed by Müller who concluded that the nearer one approached the axis of the eye, the smaller was the number of percipient elements connected with a ganglionic cell and an optic nerve fibre. In fact, he foresaw the individual conductibility in the foveal region, though he was unable to prove it.

To resume, the fovea is a region in which cones only occur: these are very thin and compressed together, especially at the centre of the region. The special arrangment of the cone-granules in several strata is a consequence of the increase in the number of cones in the unit area. Since the foveal cones are thin and rod-like, and in order that a great number of them may be packed in this area of most acute vision, it is clear that their granules, or cellular bodies, cannot all be immediately adjacent to the inner segments of the cones themselves. This explains why, in the foveal region, the cone-granules occupy various positions in the outer granular layer, exactly as in the case of the rod-granules in the rest of the retina. Moreover, in the foveal region, each bipolar cell is connected with a single cone-granule and not with several as in other parts: hence a necessary increase in the thickness of the inner granular and of the ganglionic layers; but the thickening of these layers would prevent light from easily reaching the percipient elements; the existence of the fovea, i.e., of a depression in which the inner retinal layers are shifted aside, gives the required thinness and transparency.

Only man and the highest apes have a true fovea; in most vertebrates (except fishes) the retina presents an "area" which is a thickened portion where the histologic disposition is somewhat similar to that observed in the macula of the human retina and where visual acuity has probably the highest value. There is an increase in the thickness of the outer granular layer and of the ganglionic layer and, at the same time, the percipient elements are more closely packed. It is logical to assume that, owing to the process of gradual evolution, the area would become too thick for the proper

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working of this part and that the formation of the foveal depression is intended to supply the necessary thinness and transparency. This seems to be proved by the fact that in the human embryo, there is only an "area" up to the sixth month when the fovea begins to appear. Considering what has been said it is clear that the fovea may be regarded as an area which has become depressed in view of a more perfect performance of its function.

The area does not always occupy the centre of the retina. Thus, in the dog, it is a little above and on the temporal side of the papilla: it is therefore very externally placed, since the dog's papilla is on the temporal side of the posterior pole.

In the fundus of the horse, the vascularised part of the retina extends but a short distance round the papilla. Immediately above the papilla the area is seen in the form of a transversal light band which is the inferior limit of the tapetum.

**The Retinal Neurons.**

To complete our study of the minute structure of the retina, we must say a few words on the subject of the interconnection of the retinal elements. We have already stated that there is no direct anatomical or structural continuity of the several retinal layers. As with the other parts of the nervous system, the nerve-elements of the retina are isolated units merely coming into connection with one another by the interlacement or contiguity of their arborescent processes, and not by direct continuity.

In the case of cones, the cone-fibres end in flattened expansions or cone-feet from which fine processes extend in the outer molecular layer. Immediately opposite these processes, but not in actual continuity, lie the outer processes of a bipolar cell. The inner end of the bipolar cell processes terminates in expanding branches in the inner molecular layer where it articulates with the dendrons of a ganglionic cell. The axon of that cell is, on the other hand, connected with an optic nerve fibre.

In the case of a rod, the rod-fibre ends in a knob in the most external part of the outer nuclear layer: this knob is surrounded by the arborescent processes from the outer pole of a bipolar cell while the process from the inner pole of the cell terminates in arborisations surrounding the body of a ganglionic cell. The axon of the ganglionic cell is continuous with an optic nerve fibre.

Thus, rods and cones are brought into relationship with the optic nerve fibres. The path of connection shows two

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breaks or, as they are usually termed, two synapses in the structural continuity. In the case of a rod, these breaks occur in the outer molecular layer and in the ganglionic layer respectively. In the case of a cone, in the outer and the inner molecular layers. It must be well understood that these structural breaks or synapses do not prevent the passage of nervous impulses.

It follows, from what has been said so far, that the retina is essentially formed of a number of nerve cell chains, or neurons, arranged in three series from without inwards. The first visual neuron is formed by the rod or cone element, i.e., by the rod or cone proper with its granule and its fibre: it constitutes the highly differentiated sensory epithelium of the retina. The second visual neuron consists of the bipolar cell with its system of outer processes articulated with the rod- or cone-fibre and its system of inner processes articulated with the outer dendritic processes of a ganglionic cell or with the body of the cell as the case may be. The third visual neuron is made of the ganglionic cell, the dendrons of which are articulated with the processes from the inner pole of a bipolar cell while its axon is continuous with an optic nerve fibre.

The first visual neuron is the neuron of reception or the peripheral sensitive neuron. The portion of the retina it occupies (layer of rods and cones, outer nuclear layer and outer molecular layer) does not contain any blood-vessels: the nutrition of these layers takes place by osmosis, the source of supply being the choriocapillaris layer of the choroid. The second and third visual neurons are neurons of transmission and the nutrition of the corresponding retinal layers is insured by the capillary vessels derived from the central artery of the retina. The second neuron is often termed the intermediate and the third, the central or retino-ganglionary neuron.

We have pointed out that in molluscs the retina is reduced to the first neuron, the other two being in the optic lobe of the brain. Moreover, in our brief study of the various sense-organs from the simplest one (sense of touch) to the most complex, namely, the organ of sight, we have seen that the general arrangement is fairly constant. In the sense-organ of touch and in that of taste, the sensory epithelium, i.e., the tactile corpuscles and the gustatory cells, occupy the surface (skin and mucous membrane of the tongue and mouth) but the cellular body of the neuron of reception lies far from the surface and is found in the ganglion of the posterior root of a spinal nerve in the case of the

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sense-organ of touch and in the nucleus of the glosso-pharyngeal nerve in the case of the organ of taste. In the more complex organ of hearing, the differentiated sensory epithelium is constituted by the cells of the organ of Corti, which lies in the internal ear, and the cellular body of the neuron of reception is much nearer the periphery than is the case in the organs of touch and taste. In the organ of sight, not only the neuron of reception and the intermediate neuron are near the periphery, i.e., within the retina, but the central neuron which, in other sense-organs lies in the cerebro-spinal axis, is also within the retina.

This arrangement is, as we have already stated, calculated to insure an easier, quicker and more perfect answer to external stimuli. Beside, it justified the view, supported by embryological considerations and by comparative anatomy, that the retina is really a nervous centre, a portion of the brain which has pushed its way out of the cranial cavity and it follows that the optic nerve is not comparable to an ordinary peripheral nerve but is really a commissural tract connecting two nervous centres, namely the cerebral portion of the retina, i.e., the ganglionic layer (the cells of which may be assimilated to those of the grey matter of the ordinary nervous centres) and the grey matter of the primary visual centres.

In our present description, we have traced the path of visual impressions through the three neurons which form a chain extending from the rods and cones on one hand to the optic nerve fibres on the other hand. We have pointed out repeatedly that the fibres of the optic nerve after passing through, and partly decussating in, the chiasma, apparently end in the primary or basal visual centres, namely the external geniculate and the anterior quadrigeminal bodies. Another visual neuron, the intracerebral neuron of transmission, connects the primary visual centres and the visual centre in the cerebral cortex of the occipital lobe, as we shall see presently.

It should be borne in mind that, whatever the nature of an external stimulus acting on the retina, the nervous impulse generated in the sensory epithelium can only give rise to a visual sensation. The normal or, as it is often termed, the adequate stimulus of the retina is light, but if any other stimulus be applied to it, the response is a luminous sensation. This is shown by the luminous phenomena occurring when an electric current is made to pass through the retina or when a pressure is applied to the globe (phosphene). A similar remark applies to the other sense-organs: for instance, if the acoustic nerve or the organ of Corti be

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artificially stimulated, a sensation of sound results, and again, sensations of smell may arise, apart from the existence of a smelling object, when the olfactive membrane is artificially stimulated, as occasionally happens in some diseases of the nose.

The chain of neurons we have just studied constitutes what might be termed the apparatus of centripetal conduction. The visual impulses generated in the sensory epithelium, i.e., in the layer of rods and cones, are carried by the axons of the ganglionic cells to the primary visual centres.

We have seen that the bipolar cells and their processes constitute a connection between the visual cells (first neuron) and the ganglionic cells (third neuron) and that, except at the fovea, there is a gradual reduction in the number of conductors from the outer to the inner retinal surface. Thus, one of the large bipolar cells may be articulated with the terminal knobs or with the cone-feet of fifteen to twenty visual cells while the smaller bipolar cells are articulated with only two or three visual cells. It follows that the outer molecular layer, which is the zone of articulation of the first and second neuron, i.e., of the visual cells and the bipolar cells, is a zone of reduction in the number of conducting elements. In the same way, and again except at the fovea, a single ganglionic cell may be articulated with several bipolar cells, but in the foveal area each cone has its own bipolar and probably its own ganglionic cell, since we have seen that the number of ganglionic cells increases considerably at the edge of the depression.

According to Krause, there are 130 million rods and 7 million cones in the human retina while the number of optic nerve fibres does not seem to be above 800,000. Whatever the uncertainty of these figures, the discrepancy between the number of optic nerve fibres and that of percipient elements is striking and is a proof of the reduction stated just now.

In addition to the true centripetal optic fibres, there are in the optic nerve large centripetal fibres termed the pupillary fibres the purpose of which will be explained presently. Beside, Cajal has demonstrated the presence in the optic nerve of a set of centrifugal fibres originating from the primary visual centres, and perhaps from the cortex, and passing into the optic tract and the optic nerve together with the true optic (centripetal) fibres to end in the inner nuclear layer, where they seem to be articulated with the amacrine cells. They are supposed to transmit orders from the brain, to produce the voluntary adaptation of the retina, i.e., the phenomenon termed attention.

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We shall see also, presently, that in some of the higher mammals there is a bundle of fibres, constituting what is termed the anterior commissure of Gudden, which connects the two retinæ through the chiasma. These fibres are not visual fibres in the ordinary sense of the term but merely association fibres between the third neuron of the right retina and the third neuron of the left retina. This commissure is completed by Gudden's posterior commissure which is formed by a small bundle of fibres extending from one external geniculate body to that of the opposite side through the chiasma. The existence of these commissures in the human being is regarded as doubtful.

Likewise, there are association bundles connecting various areas of the cerebral cortex, for instance, the motor area concerned with the voluntary movements of the limbs and head (near the fissure of Rolando), the centre for speech in the left hemisphere, and the true visual centre in the occipital lobe of each hemisphere, near the calcarine fissure. The visual centre of one hemisphere is also connected with that of the other hemisphere by commissural fibres forming part of the corpus callosum.

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## CHAPTER XIV.

### MICROSCOPIC STRUCTURE OF THE OPTIC NERVE, THE CHIASMA, OPTIC TRACTS AND VISUAL CENTRES.

**The Minute Structure of the Optic Nerve.**

We have pointed out before that the optic nerve exactly fills the scleral canal, i.e., the opening in the sclerotic and choroid through which it emerges from the globe. The fibres forming the various bundles of the optic nerve are deprived of their myeline sheaths in the scleral canal and in the retina. The lamina cribrosa, examined on an antero-posterior section, appears as made of a system of transversal bundles of connective tissue, extending from one edge of the scleral canal to the other in a slightly curved direction, the concavity of which is turned towards the eye. This concavity varies, physiologically, but never reaches the high degree observed in glaucomatous affections. At a first glance, the lamina cribrosa appears to exist only in the posterior half or two-thirds of the canal; this is due to the fact that the strongest part of the lamina is formed by scleratical fibres but, at the level of the ocular orifice of the scleral canal, the choroid also supplies thin bundles forming what might be called a delicate choroidal lamina cribrosa, to distinguish it from the stronger sclerotical lamina. In many animals (dog, sheep, horse, etc.) the lamina cribrosa is relatively weak and reduced to little more than the choroidal part. In man, it is much stronger and consists distinctly of a choroidal and a sclerotical portion.

The structure of the optic nerve is the same in the orbital, the canalicular, and the intracranial portions. At the level of the posterior surface of the lamina cribosa the optic fibres acquire their medullary sheaths, the trunk of the nerve increasing in volume almost suddenly and passing from a diameter of 2 mms. to one of about 4 mms.

The trunk of the nerve consists of a large number of bundles separated from one another by fibrous septa and connective tissue. The protective sheaths of the nerve have already been studied. The individual nerve fibres are separated and supported by a delicate neurogliar tissue.

There are, in the optic nerve, fibres of very different sizes. The largest have a diameter of 5 to 10 microns, whereas the finest reach an almost incommensurable smallness. These differences are easily explained: the multipolar or ganglionic cells of the retina are of widely different sizes,

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the macular ones being very small, the peripheral ones larger; it is, therefore, not surprising to find that the cylinder-axes of these cells are of corresponding sizes. Beside, independently of the ordinary "optic" fibres, there are in the optic nerve centrifugal fibres travelling from the nervous centres to the retina: these fibres are relatively small; finally, there are also voluminous centripetal fibres (pupillary or photo-motor), which we shall investigate presently.

The question of the number of fibres in the optic nerve has lost its interest since we know that the nerve is not made of visual fibres only. If it were so built, it would be interesting to compare the number of fibres with that of the rods and cones, but the existence of the centrifugal and of the centripetal photo-motor fibres as well as that of the commissural fibres renders the comparison useless. Suffice it to say that the number of fibres is enormous. The estimate of Kuhne who gives 40,000 appears to be very much below the truth. It is probable that Krause is nearer the mark with his estimate of 800,000. The wide discrepancy between the above figures shows the little value we may attach to them.

**The Optic Chiasma.**

The nervous mass of the chiasma contains the same elements as the optic nerve except that the connective tissue septa are less numerous; in fact, in the nervous centres the connective tissue is almost entirely absent. From the reduction in the number, and, ultimately, from the disappearance of the septa, it follows that the nervous fibres are not grouped in bundles as in the optic nerve; they are so intimately interlaced that it is impossible to trace their path with certainty by simple dissection and observation; even the ordinary staining methods are unable to elucidate the subject of the path of the optic fibres in the chiasma. In their interpretation of sections, the first anatomists who studied the subject were biased by preadmitted notions on the constitution of the chiasma, or again, they applied to man the results of examination of lower animals. Even such an authority as Kolliker rejected the idea of direct fibres on the pretext that anatomical examination was unable to demonstrate their existence.

The constitution of the chiasma had been postulated by Newton a long time before the introduction of the modern methods of investigation. Newton (1704), trying to explain single binocular vision, thought that the fibres of the right sides of the two retinæ were united in the right tract; those

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of the left halves, in the left tract. He added "these two nerves (or tracts as they are now called) must be so united in the brain that their fibres give rise to a single image, the right half of which comes from the right side of each eye, the left half from the left side of each eye." He saw a proof of his hypothesis in the fact that "in animals which look at an object with the two eyes, the two optic nerves are partly united before entering the brain whereas the optic nerves of animals the two eyes of which do not look at the same object (fishes) are not so united, the nerve of each eye passing to the opposite side of the brain."

The postulatum of Newton, based on a physiologic necessity, contained (1) the theory of half decussation in animals with binocular vision; (2) the necessity of a means of union between the two cerebral hemispheres in order to permit the juxtaposition of the two hemiopic fields; (3) the theory of complete crossing in animals with panoramic vision.

The old histologic methods being insufficient, Ramon y Cajal applied Golgi's method to the study of the chiasma. He found a complete crossing in fishes and batracians; in the former, the two nerves simply pass one above the other; in the latter, one optic nerve passes through a slit in the other. In amphibia and birds, the crossing is also complete; each nerve divides into a number of flat bundles which all pass over to the other side, interlacing with the bundles of the opposite side as they cross, in the same fashion as the intertwined fingers of two hands when clasped together.

Thus, the complete crossing is the rule in lower animals, but it must not be assumed that the condition holds good for the higher vertebrates. In mammals like the rabbit or the rat, the chromate of silver method does not always show the existence of direct fibres and, therefore, complete crossing might be thought to exist, but the degeneration method shows clearly that there are some direct fibres. In the cat, however, the direct fibres are easily detected by the chromate of silver; they represent almost a third of the volume of the nerve and though most of them lie in the external part of the nerve a few pass near the centre of the chiasma.

To sum up, in higher vertebrates a partial decussation occurs, the partial character of which is more pronounced the nearer akin the animal is to man. In man, the non-decussating bundle approximates the decussating one in size, the former containing about two-fifths and the latter three-fifths of the total number of optic nerve fibres. In a general way, the direct or uncrossed fibres seem to occupy the upper portion of the chiasma whereas the crossed fibres pass through



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the inferior portion. By means of improved methods of staining, Cajal found, in some animals, a number of bifurcated fibres: such a retinal fibre divides into two equal fibres on entering the chiasma, one of them passes into the opposite tract, the other into the tract on the same side. It has been suggested that these bifurcated fibres proceed from the macula and that their existence would explain the fact (to which we shall revert presently) that the macula of each eye is connected with the two cerebral hemispheres. This assumption does not appear to be fully justified since bifurcated fibres have not been observed in the human subject.

Even the most modern histologic methods have not entirely settled the question of the constitution of the chiasma. We shall see presently that the degeneration method furnishes very important data on the subject.

**The Primary Visual Centres.**

On entering the tracts the optic fibres resume the parallel direction they had in the nerves. The tracts do not show the septa of connective tissue we have mentioned in the case of the optic nerves; in fact, the connective tissue is even less abundant in the tracts than in the chiasma, the fibres being separated from each other by neuroglia. As already stated, each optic tract appears to end partly in the external geniculate body and partly in the anterior quadrigeminal body. Examination and dissection cannot supply definite information as to the course of the optic fibres in the tracts and in the basal ganglia; even the modern staining methods are insufficient. As we shall see presently, after enucleation of both eyes, especially in a newborn animal, it is found that neither the internal geniculate nor the posterior quadrigeminal body is affected with degeneration: hence, the external geniculate and the anterior quadrigeminal only are visual centres. We will come again to the subject in sketching the results furnished by the degeneration method. This method has also shown that the ganglia of the base of the brain are connected with the cortex of the occipital lobe by fibres, forming what is known as the optic radiation.

**The Cortical Visual Centre.**

Though we have given (page 68) a brief description of the cerebral cortex generally, a few supplementary remarks may be useful. The details of structure vary according to the portion that is being considered, but we cannot enter into these differences and must be content with a somewhat diagrammatic description of the cortex as a whole.

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The grey matter of the convoluted surface of the cerebral hemisphere forms a continuous covering about 3 to 4 mms. thick, which is divided into several strata by interposed thin layers of paler substance. On examining a section with the naked eye, we can recognise, from without inwards: (1) A thin coating of whitish matter situated on the outside surface and appearing on the section as a faint line bounding the grey surface externally. This layer is not equally thick everywhere: it is more conspicuous on the under surface of the brain. (2) Immediately beneath the white layer just mentioned is found a layer of grey or reddish matter, the colour of which is deeper or lighter according as its numerous vessels contain much or little blood. (3) A layer appearing as a thin whitish line (line of Vicq d'Azyr). (4) A second grey stratum. (5) A second thin whitish line. (6) A yellowish-grey layer which lies next to the central white matter of the convolution. In some parts, as in the neighbourhood of the calcarine fissure (occipital lobe) the line of Vicq d'Azyr is very distinct but the 5th layer is not visible.

The minute structure of the cerebral cortex has been investigated with sufficient detail for our purpose. Let it be remembered that the nervous cells of the grey matter of the cortex are embedded in a supporting tissue, or neuroglia, through which the fibres pass to and from the cells. The neuroglia is more marked in the outermost parts of the cortex immediately below the pia mater, and since, in a section, its wavy fibres are mostly seen as sectional dots, this portion is termed the molecular layer. Internally to this layer, the cortex is characterised by the presence of nerve cells whose shape is roughly pyramidal with the apex pointing toward the surface of the brain. This layer may, therefore, be called the layer of pyramidal cells; the cells vary in size in the several strata of the layer, the largest being found in the deeper portion, the smallest next to the molecular layer. The part of the cortex which lies immediately external to the central white matter is characterised by the presence of nerve cells of a somewhat irregular and variable form; hence this layer is known as the layer of polymorphous cells. Beneath this last layer is the white matter, the medullary fibres of which become finer as they radiate into the grey matter and are mostly continuous with the cylinder-axes of the pyramidal cells. These fibres pass either as association fibres to other parts of the cortex of the same hemisphere, or as commissural fibres through the corpus callosum to the opposite hemisphere, or as projection fibres to the ganglia of the base, or finally, by way of the internal capsule, to the bulb and the spinal cord

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## CHAPTER XV.

### THE PATH OF VISUAL IMPULSES GENERALLY.

Anatomical dissection and microscopic examination are insufficient to enable us to trace the path of visual impulses beyond the primary centres.

Let us now examine what can be learnt as to the path of visual impulses by the degeneration method and by the anatomo-clinical method.

**The Path of Visual Impulses Studied by the Degeneration Method.**

It has long been known that the destruction of an eye determines the atrophy of the corresponding optic nerve, and that this "ascending" atrophy extends to the ganglia of the base of the brain, but it was Gudden who was the first to make a systematic study of the subject (1872) and who showed in this way that only the external geniculate and the anterior quadrigeminal are visual centres. A little later (1888) Von Monakow completed Gudden's work. Not only did he study the ascending degeneration from the eye to the ganglia of the base after enucleation, but he also removed or destroyed some limited portions of the occipital cortex and observed descending degeneration from the cortex to the basal ganglia, thus determining completely the path of the optic fibres.

Von Monakow's researches have chiefly been made on new-born and adult animals (rabbits, cats, dogs). In some small details the optic path of these animals differs from that in man, but the fundamental scheme is the same in both cases. Therefore, neglecting details which do not apply to human anatomy, we reproduce, in a somewhat simplified form, the diagram which resumes the whole work (fig. 24).

Let it be remembered that we have given the name of "neuron" to a nervous cell with all its processes, dendrites and axon. If the axon of a neuron is sectioned, the peripheral end of the fibre, that is, the end no longer connected with the cell, degenerates, i.e., dies, exactly as does a branch separated from its tree. This degeneration, which is a gradual disorganisation of the nervous fibre from the point of section, progresses up to the final ramifications. The degeneration shows itself by structural changes which have been mentioned. While these changes take place, and even before they are obvious, the irritability of the fibre gradually becomes less, and finally it completely disappears. The

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phenomenon is often termed "Wallerian degeneration," as it was described for the first time by Augustus Waller in 1852 (see page 47).

The diagram of Monakow (fig. 24) is almost self-explanatory. In a young animal, say, a rabbit, the extirpation of both eyes determines a degeneration of both optic nerves and tracts and atrophic lesions localised in certain

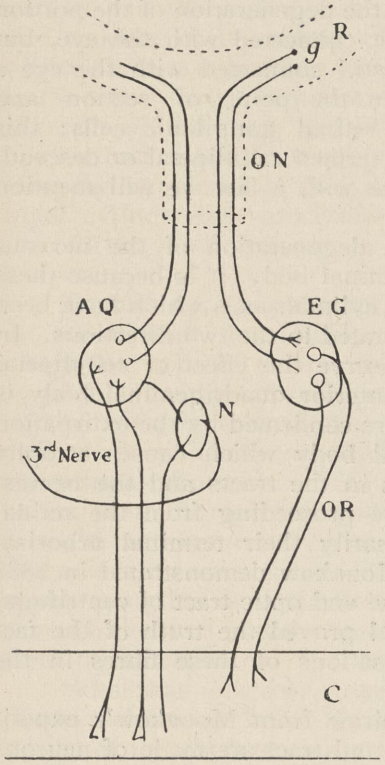


FIG. 24.

FIG. 24. DIAGRAM OF MONAKOW. Showing, in a diagrammatic form, the centrifugal and centripetal connections of the retina, the primary visual centres and the cortical centre.

R is the retina; O N the optic nerve and tract; E G the external geniculate body; A Q the anterior quadrigeminal body; N the nucleus of origin of the third nerve; O R the optic radiation; C the cerebral cortex in the neighbourhood of the calcarine fissure. The axons of the ganglionic cells of the retina (*g*) continued into the cylinder-axes of the optic nerve fibres pass into the external geniculate body, where they are physiologically connected by synapses with the cells of the geniculate, which are the origin of the fibres of the optic radiation O R. In the cortex, these fibres are connected, no doubt by means of intercalar cells, with other cellular elements, especially the large pyramidal cells. The axons of the pyramidal cells of the cortex travel via the optic radiation to the anterior quadrigeminal body; there they arborise, i.e., form synapses, with the cells of the quadrigeminal, the axons of these cells travelling via the optic tract and the optic nerve to end in the retina, probably in the inner molecular layer.

The nucleus of the third nerve N is connected with the anterior quadrigeminal body, and with the pyramidal cells of the visual cortex.

parts of the external geniculate body and of the anterior quadrigeminal body. In the geniculate, what degenerates is the gelatinous substance, i.e., the plexus formed by the terminal arborisations of the tract, but the nervous or ganglionic cells themselves are preserved. In the anterior quadrigeminal body, what disappear are the nervous cells of that ganglion. What is the significance of these changes?

If enucleation (or a section of the optic nerve) causes degeneration of the gelatinous substance of the external

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geniculate, it is because it causes degeneration of the cylinder-axes of the nerves and tracts, the terminal arborisations of which form the gelatinous substance of the ganglion in question. The degeneration is cellulifugal, ascending, (extending towards the brain), the cells from which these cylinder-axes proceed, i.e., the ganglionic cells of the retina, occupying the other extremity of the cut nervous bundle. In the case of a simple section of an optic nerve, not only do we observe the degeneration of the portion of the nerve that is no longer connected with the eye, but we also observe in the part still connected with the eye a degeneration proceeding from the point of section and extending ultimately to the retinal ganglionic cells; this second degeneration which is termed cellulipetal or descending, takes place in accordance with a law we will mention presently.

Since enucleation causes degeneration of the nervous cells of the anterior quadrigeminal body, it is because these cells send into the optic nerve cylinder-axes which have been cut and have therefore degenerated in the two directions. In the actual experiment, we observe the effect of cellulipetal degeneration, so far as the anterior quadrigeminal body is concerned, and these results are confirmed by the extirpation of the anterior quadrigeminal body which causes atrophy of a certain number of fibres in the tracts and the nerves. These fibres (finer than those proceeding from the retinal ganglionic cells) have necessarily their terminal arborisations in the retina. Thus, Monakow demonstrated in 1888 the existence in the optic nerve and optic tract of centrifugal fibres; a few years later Cajal proved the truth of the fact and saw the terminal arborisations of these fibres in the inner nuclear layer.

The first conclusion to draw from Monakow's experiments is that the optic nerve and tract are made of neurons extending from the retina to the external geniculate body and the anterior quadrigeminal body; these neurons form the anterior segment (partly extra-cerebral) of the optic path. Moreover, this path is double and made of: (a) centripetal fibres (from the retina to the external geniculate); (b) centrifugal fibres (from the anterior quadrigeminal body to the retina).

Monakow went further and showed that removal or destruction of the part of the cerebral cortex occupying the occipital lobe determines: (1) atrophy of the ganglionic cells of the external geniculate; (2) atrophy of the fibres of the white matter of the anterior quadrigeminal body. The destruction of the cortex has therefore caused a cellulipetal

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degeneration in the external geniculate whose large cells have disappeared and a cellulifugal degeneration in the anterior quadrigeminal, some nervous fibres of which have become atrophied.

On the other hand, a section of the internal capsule, along which passes the optic radiation, causes: (1) between the section and the basal ganglia, a degeneration similar to that following the destruction of the cortex; (2) between the section and the cortex, a degeneration reaching the cortex and causing in it atrophy of the large pyramidal cells. Hence these conclusions:—(a) From the ganglia of the base to the visual cortex, neurons extend which form the posterior segment of the optic path. (b) This part of the path is double and made of centripetal cylinder-axes proceeding from the large cells of the external geniculate, and of centrifugal cylinder-axes proceeding from the pyramidal cells of the cortex and ending in the anterior quadrigeminal body.

To sum up, the optic path from the retina to the cortex is constituted as follows:—(a) Centripetal direction; ganglionic cells of the retina and their cylinder-axes going to arborise in the external geniculate and entering into connection with the cells of this ganglion. In their turn, these cells send cylinder-axes which arborise in the cortex. (b) Centrifugal direction. The large pyramidal cells of the cortex send through the optic radiation their cylinder-axes into the anterior quadrigeminal body where they arborise and enter into connection with the cells of the grey substance of this ganglion, and the latter cells send their cylinder-axes through the tract and the optic nerve into the inner granular layer of the retina.

What has just been said is a brief abstract of Von Monakow's researches. He taught us at the same time the results of the degeneration method applied to the optic path and the laws governing these degenerations. We know now that when a bundle of fibres is cut or pathologically destroyed, we observe at one extremity the degeneration of a reticulum, and at the other extremity the atrophy of a cellular group. The conclusion to draw from this is that the degenerated cells represent the origin of the cut cylinder-axes while the reticulum which degenerates at the other end of the bundle is but the collection of their terminal arborisations. In other words, and supposing that the method could apply to a single element, i.e., to a single neuron, the section of a cylinder-axis not only involves the degeneration (Wallerian or cellulifugal or ascending) of the extremity separated from the cell but also (though more slowly and

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less completely) the degeneration of the end attached to the cell and of the cell itself (cellulipetal or descending degeneration).

Originally, the reduction of volume was the only way of recognising the degenerated part; thus, Gudden measured the area of section of the two tracts to find out whether one only or both had lost their normal thickness. Nowadays, coloration methods have been devised which permit a distinction between degenerated and healthy elements. One of the best is the method of Nissl, consisting in coloration with a warm solution of methylene blue and discoloration by a mixture of alcohol and aniline oil. The method had been applied first to the study of the ganglionic cells of the retina. It showed that in a protoplasmic, colourless mass, probably of reticular structure, blocks of chromophile (i.e., readily stained) substance, strongly coloured in blue, are embedded. The large protoplasmic processes or dendrons of the cell have the same structure as the cellular body, and show the chromophile substance in the form of grains or small rods. The cylinder-axis or axon is absolutely free from chromophile grains, its substance continuing the colourless or achromatic substance of the cell. Most probably, it is the colourless part of the cell which possesses the power of conductibility, the chromophile blocks being nutrient materials which are used up during cellular activity and regenerated by rest.

The nucleus of a normal nervous cell occupies a central position. When the cylinder-axis is cut, the alterations in the cell are clearly shown; the chromophile substance is disintegrated, i.e., to a certain extent dissolved instead of forming disseminated blocks; the nucleus takes a more excentric position and, at a later stage, it completely disappears. These phenomena appear a few days after the section of the cylinder-axis and it is clear that it is possible, in this way, to determine the nervous cells of origin of a bundle of fibres cut experimentally or destroyed pathologically.

The method of Nissl only applies to cellular elements; there is, up to now, no method of coloration for degenerated fibres, but as the degeneration of a fibre is accompanied by visible structural changes, including a breaking up of the myeline sheath into oily drops which may be coloured by diluted osmic acid, it is possible to follow the track of degenerated fibres, at least as far as they are covered with myeline.

As we have seen, a wounded neuron dies gradually in all its length. Beside, the death of a neuron may cause the death of other neurons with which it is connected. This

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secondary or tertiary degeneration, i.e., degeneration extending to the second or third link of a neuron chain, occurs more slowly. Thus, the enucleation of both eyes in newborn animals, or their pathological destruction in young children, determines a rapid degeneration of the anterior segment of the optic path (nerves, tracts and external geniculate bodies) and a slower degeneration of the posterior segment shown by reduction in the optic radiation and in the cortex.

Not only do all the neurons of a same chain degenerate, but the association bundles, uniting the system originally degenerated with other systems, may also degenerate. For instance, it has been observed, in an old standing case of destruction of both eyes in a leper, that the atrophied part of the cortex was not only the occipital visual centre, but that the degeneration extended to the parietal and to the temporal lobes. This can be explained by the fact that the occipital centre is normally united, through association bundles, with other cerebral centres and that the inactivity and degeneration of the former extend to the latter.

It must be understood that while the degeneration method enables us to understand the connection of the different parts of the visual apparatus, it would not be wise to draw conclusions as to the functions of these parts. For instance, from the fact that the optic radiation appears to spread into the whole of the occipital lobe, we cannot conclude that all the occipital convolutions have visual functions. Only by the anatomo-clinical method can we recognise the functional value of the different parts of the visual apparatus. Obviously, this method is not practical in the case of animals as the visual troubles caused by experimental lesions are of a too difficult interpretation.

The degeneration method gives important data on the constitution of the chiasma. As we have seen before, a double enucleation in a young animal had led Monakow to determine the path of visual impulses from the eye to the brain. Enucleation of one eye only shows which of the fibres of the optic tract degenerate and which do not; it enables us, therefore, to find out the part played by each optic nerve in the constitution of the optic tracts and to elucidate the question of partial or total decussation in the chiasma.

Beside, limited lesions of the retina, such as destruction of some parts by the galvano-cautery, will show that the juxtaposed retinal elements conserve their respective positions in the optic nerve.

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From numerous observations on animals, we can conclude that in those animals with panoramic vision, i.e., with two separate visual fields (a condition which occurs in animals the two eyes of which are placed so laterally that there is no common or binocular part of their fields) the crossing of the optic nerves is complete, whereas it is more or less partial in those animals the two fields of which more or less overlap, i.e., in animals with a more or less extensive binocular field of vision.

In the rabbit, the guinea-pig, and the rat, almost all the fibres of the degenerated nerve may be traced into the opposite tract, only a few passing into the tract of the same side. In the cat three-fifths of the degenerated fibres of the cut optic nerve pass into the opposite tract, and two-fifths into the tract of the same side. In monkeys, the direct fibres are almost as numerous as the crossed ones.

The situation in a section of the optic nerve of the fibres proceeding from the different parts of the retina has been ascertained by the method stated above and it has been found that the different regions of the retina correspond, point by point, to the corresponding regions of a transversal section of the optic nerve on the same side and of the tract on the opposite side. Thus, the external region of the right retina sends its fibres into the external part of the right nerve and into the internal part of the left tract (law of topographic homology).

In man, as we have already pointed out, a double enucleation causes degeneration of the anterior segment of the visual path, i.e., optic nerves, optic tracts, external geniculate and anterior quadrigeminal bodies. A secondary degeneration of the posterior segment, i.e., optic radiation and visual cortex, occurs more slowly.

The results of the enucleation or destruction of one eye only have been particularly studied by Cramer, whose conclusions are confirmed by many similar observations made since. Cramer's subject was a man of 60 whose right eye had been destroyed 18 years previously. Sections of the nerves and of the chiasma showed that the right optic nerve, much reduced in volume, was completely deprived of nervous fibres; the left was normal and its fibres, as they reached the chiasma, were divided into two bundles; the most numerous traversed the chiasma obliquely from left to right to penetrate into the right tract, the greater part of which they constituted. They represent the crossed bundle of the nerve. The rest of the fibres of the left optic nerve, less numerous, passed to the left tract, and were the only fibres left in that tract. On following the degeneration in the tracts, it was

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found that, in the right tract, containing the direct degenerated fibres, these chiefly occupied the centre of the bundle. In the left tract, the crossed degenerated fibres occupied the inferior part. In the chiasma itself, the crossed fibres passed through the bottom of the chiasma, the direct fibres through the top.

Both the external geniculate bodies were affected by the degeneration, but the left one (crossed with respect to the degenerated nerve) was more affected than the right one; this is again a proof of the predominance of the crossed bundle. The crossed bundle radiated in the superficial part of the ganglion; the direct bundle, in the central portion. In the case of the anterior quadrigeminal bodies, the degeneration was also more pronounced in the crossed than in the direct ganglion; the reduction in volume was more apparent in the superficial layers, which would lead to the conclusion that the anterior quadrigeminal bodies are only connected with some optic nerve fibres through their superficial part; the other layers, probably more important, are connected with the optic radiation.

The above results, due to Cramer's researches, have been confirmed by more recent observations. Beside establishing clearly the connections of the optic nerve fibres with the basal ganglia, they leave no doubt as to the semi-decussation theory.

**The Papillo-Macular Bundle.**

Our study of the path of visual impulses would not be complete if we did not say a few words on the papillo-macular bundle of the optic nerve. The discovery of this special and most important bundle of the optic nerve results from what is termed the anatomo-clinical method, i.e., from the observation of a well-defined lesion, namely, degeneration of a special bundle of the optic nerve in the case of an equally well-defined symptom, namely, central scotoma. Leber, observing (1869) the discoloration of the temporal part of the disc in a case of central scotoma, concluded that the fibres ending in the fovea and the surrounding area are grouped in the temporal part of the optic nerve. This hypothesis was confirmed by observation of microscopic sections of the optic nerve of subjects who, before death, had a double central scotoma. It is now proved that the macular bundle occupies a determined position in the whole length of the anterior segment of the visual path and that, in the chiasma, the right and left macular bundles fuse to undergo a decussation similar to that of the nerves themselves. This conception is based: (a) on the fact observed in case of

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degeneration when the two atrophied bundles are seen fused in the centre of the chiasma; (b) on Newton's postulatum concerning single vision with the two eyes since the postulatum especially concerns direct vision; (c) on the conservation of central vision in both eyes in cases of destruction of the occipital cortex of one hemisphere only. In such cases, it is a physiologic necessity that the occipital lobe left intact may suffice to the innervation of both maculæ.

The degeneration method has been used by Henschen and others to ascertain the situation of the different bundles of fibres in the optic nerves, the chiasma and the tracts. The results of their researches may be resumed as follows:—

(1) The macular bundle, on leaving the globe, occupies the infero-external part of the nerve, exactly as, in the retina, the macula occupies the infero-external side. It soon passes into the central part of the nerve (immediately beyond the point of entry of the central retinal vessels) and keeps that position in the nerve, the chiasma and the tracts. In the centre of the optic chiasma, the decussating fibres of the two macular bundles appear to cross each other on the median line, whereas the direct fibres seem to occupy the external parts of this little macular chiasma. There is, however, no anatomical or clinical evidence of the existence of this macular chiasma. No cases have ever been recorded of macular hemianopsia and, as we shall see presently, Cajal has observed bifurcated fibres at the centre of the chiasma of some animals, these fibres being perhaps those of the papillo-macular bundle which thus would insure a direct connection between the fovea of each eye and the two cortical centres. Though these bifurcating fibres have only been observed so far in the eyes of animals (like the rabbit) which have no binocular field of vision, yet the fact that they have not been discovered in the human eye may be due to the imperfection of our present histological methods. (See page 276.) We must not overlook the fact that in all cases of homonymous hemianopsia which have been recorded, the fovea is always included in the seeing half of the retina.

(2) The crossed bundle, proceeding from the nasal half of the right retina, occupies the infero-internal part of the right optic nerve up to the chiasma. There, the fibres of the two crossed bundles occupy the central part, round the macular chiasma. In the tract, the crossed fibres occupy the infero-internal part.

(3) The direct fibres, from the temporal half of the right retina, occupy also the external part of the right optic nerve. Very near the globe, the macular bundle which has not yet reached the central part of the nerve, and is still on the

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external side, divides the direct bundle into two branches, a superior and an inferior one, which unite in the external part of the nerve as soon as the macular bundle has taken its central position. In the chiasma, the direct fibres pass near the top surface. In the tract the direct bundle is above and outside the crossed one. What has been said about the right retina applies, *mutatis mutandis,* to the left one.

Thus, the optic fibres occupy in the whole extent of the anterior segment of the visual path the respective situation they have in the retina; a particular point in a section of the optic nerve corresponds to a similar position in the retina (law of topographic homology).

We have already stated that the optic tracts are connected with the external geniculate body and with the anterior quadrigeminal body. The pulvinar itself is not concerned with vision, as was thought till recently, and those cases of hemianopsia apparently caused by hemorrhage in the pulvinar are now explained by the fact that the hemorrhage is sufficiently near the external geniculate body to compress it and to prevent its proper working. The destruction of the anterior quadrigeminal body does not interfere with vision but greatly interferes with the movements of the eye and with the pupillary reactions. The internal geniculate body and the posterior quadrigeminal body do not receive fibres from the tracts as shown by the degeneration method; beside, their destruction causes no visual troubles. The external geniculate body is therefore the only true visual ganglion, the only true primary visual centre.

The problem of the determination of the visual cortical centre consists in finding the region of the cortex of a cerebral hemisphere the destruction of which abolishes the part of vision due to that hemisphere, i.e. produces bilateral homonymous hemianopsia. Here again, the degeneration method is useful, but the greater part of our knowledge of the subject is derived from the anatomo-clinical method.

**Hemianopsia.**

In dealing with this problem we must bear in mind that the vision of each eye is a function of the two cerebral hemispheres. In other words, from the point of view of the cortical function, there are not two eyes, but two right half-retinæ and two left half-retinæ, coupled together by common cortical connections. This hypothesis had been advanced almost two centuries ago to explain the curious phenomenon of hemianopsia. In 1865, Von Graefe confirmed the fact, since proved by hundreds of cases, that unilateral destructive lesions of the brain react on the two eyes to produce bilateral

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hemianopsia. This hemianopsia, this loss of the homonymous halves of the visual fields, is precisely the part of vision due to the affected hemisphere. It follows that to determine the cortical centre of one of the hemispheres, we have to find the minimum cortical lesion capable of causing hemianopsia.

**The Anatomo-Clinical Method Applied to the Study of the Path of Visual Impulses.**

It is by elimination that these researches have been made. All forms of hemianopsia due to lesions of the tracts, of the basal ganglia, and of the optic radiation have been eliminated. Then, in all cases of hemianopsia which can only be explained by cortical lesion, the location of the lesion has been ascertained. This location was verified by proving that a lesion at the point in question determined hemianopsia and that a lesion at any other point did not.

It is hardly necessary to point out the fact that hemianopsia is the projection in the field of a hemi-retinal anæsthesia; owing to the dioptric inversion of the image, this retinal anæsthesia produces loss of the opposite half of the visual field. There is often confusion in the student's mind between the terms hemianopsia and hemiopia. The former applies to a subjective symptom, namely, to the portion of the field that is lost, the latter applies to the lesion producing the symptom. Thus, left hemianopsia is loss of the left half of the visual binocular field, and this evidently corresponds to right hemiopia, i.e., to anæsthesia of the two half-retinæ which look to the left but are situated to the right of a vertical plane passing through the centre of each globe, i.e., the right (or temporal) half of the right retina and the right (or nasal) half of the left retina.

To avoid all possibility of mistake, it is well to use the term hemianopsia only, as this term is in accordance with the usual nomenclature in medical neurology. When we speak of right hemiplegia we mean paralysis of the right limbs, though we know that the cerebral lesion causing it is in the left half of the brain. In the same way, left hemianopsia is blindness for the left half of the visual field and is due to anæsthesia of the right halves of the retinæ. It should be observed that, from the etymological standpoint, the term hemiopia means half sight and not half blindness. Therefore, and strictly speaking, when we wish to convey the fact that the right halves of the retinæ are blind, we should say that there is left hemiopia since the left halves of the retinæ are seeing. By general custom, however, and in spite of its true etymological sense, the term

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right (or left) hemiopia implies that the right (or left) halves of the retinæ are blind, which corresponds to left (or right) hemianopsia, i.e., to loss of the left (or the right) half of the binocular field of vision.

Originally and essentially, the connections of the eyes with the nervous centres are crossed as is the case with the other nerves of the body, and in inferior animals this complete crossing still occurs. In the human eye, the nasal half of the left retina sends to the right tract the ancestral crossed bundle (forming the whole right tract in lower animals); the right tract is completed by the direct bundle proceeding from the temporal half of the right retina.

If we extend these notions to the visual field, we can easily understand that in all animals having two distinct fields there is crossed amaurosis and not hemianopsia as the result of unilateral cortical lesions. Hemianopsia is only possible when the direct bundle occurs, but, phylogenetically, this hemianopsia is related to crossed amaurosis.

**Location of the Visual Cortical Centre.**

It is especially since 1879 that researches have been made on the location of the cortical visual centre. About that time it became known, from clinical observations, that cortical hemianopsia was due to lesions of the occipital lobe. In 1890, Dejerine advanced the opinion that the visual centre is located in the internal surface of the occipital lobe, an opinion which had been given before (1880) by Bellouard in a thesis inspired by Panas. Bellouard's views, however, were not generally accepted as Charcot still defended, at the time, the theory of crossed amaurosis by cerebral lesions, and only admitted a lesion of the optic tract beyond the chiasma as a possible cause of hemianopsia.

Many physiologists have tried to determine experimentally the seat and limits of the visual cortical centre in animals, but the results of these experiments are in most cases of a very difficult interpretation; it is practically impossible to ascertain whether a dog is hemianopsic and whether he has lost central vision or not. For this reason, we will be content with the results of the anatomo-clinical method in man.

By successive elimination it has been possible to localise the visual centre in the occipital lobe, in the neighbourhood of the calcarine fissure. The internal surface of the occipital lobe, between the apex of the lobe and the parieto-occipital fissure, only contains three convolutions which are, going downwards, the cuneus, the lingual lobe and the fusiform lobe. The calcarine fissure separates the cuneus from the lingual lobe. In all cases of hemianopsia by cortical lesions,

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the calcarine cortex is always affected; hence the conclusion that the calcarine fissure represents the cortical visual centre. A typical case is recorded by Nordenson; it is that of a subject presenting during life a left hemianopsia; the post-mortem examination showed a lesion of the right calcarine fissure, the cortex of which was completely necrosed from the apex of the occipital lobe to the end of the fissure.

Further researches and observations have established the fact that the visual centre occupies the internal surface of the occipital lobe and that the calcarine fissure is the centre of the visual sphere which may extend to the cuneus, the lingual lobe and even to the fusiform lobe.

The subject of the projection of the retina onto the cortical centre has received some attention. Is the retina innervated in a constant and fixed manner by the cortex; that is, does a particular portion of the cortex correspond to a fixed area in the retina? The problem can only be solved by the anatomo-clinical method, and the solution is somewhat incomplete up to now. It seems well proved, however, that the superior border of each calcarine fissure innervates the homonymous superior quadrants of both retinæ; a case is recorded of a double anopsia in the form of a quadrant of the lower part of the left field and corresponding therefore to blindness of the right superior retinal quadrants; the post-mortem examination showed a softening of the upper border of the right calcarine fissure.

According to some authorities not only does the projection of the retina onto the cortex round the calcarine fissure exist for the quadrants corresponding to the borders of the fissure, but this projection exists in the most complete manner for the whole extent of the visual centre. This hypothesis is based on the fact that small, homonymous, symmetrical scotomata are occasionally observed in the two visual fields. The idea of referring them to a single central lesion is only logical. Yet, the matter is not elucidated.

The notion of a macular cortical projection, that is, of a circumscribed region of the visual cortex specially innervating the macula, is of considerable practical interest. The macular innervation in man is peculiar, inasmuch as each macula appears to be connected with the two hemispheres. In cases of hemianopsia, even when the defect is due to total destruction of the whole of an occipital lobe, central vision is maintained in both eyes; there is very little doubt, therefore, that the healthy hemisphere is sufficiently connected with the two maculæ, since the latter continue their normal functions. In other words, we are bound to admit that each macula is connected with both hemispheres. Since, on the

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other hand, we know that the whole visual region of each hemisphere is in the internal surface of the occipital lobe, the part innervating the maculæ must be included in the same area.

The exact location of the macular centre is not known, but the existence of this centre is not in doubt, considering the vital importance of macular or direct vision. The constant use and exercise of this kind of vision must necessarily bring us to admit the fact of a specialisation of a cortical region. Beside, some clinical facts point to the same direction. Cases are recorded in which, owing to a lesion of the two occipital lobes, all peripheral vision is lost in the two eyes, with conservation, more or less complete, of central vision in both; this conservation of central vision must be due to an intact island in the destroyed centres. This island may exist on one side only, that of the other side being destroyed; the fact, which has been observed clinically, confirms the idea of double innervation for each macula. If, in all similar cases, the cortical fragment remaining intact is always in a fixed position, this position will evidently represent the macular centre. The number of known cases is not yet sufficient to afford definite evidence.

The path of the optic fibres between the basal ganglia or primary centres (i.e., external geniculate and anterior quadrigeminal bodies) and the cortex of the occipital lobe, or true psychical or visual centre, is somewhat beyond the scope of this book. It is sufficient to say, for our present purpose, that fibres constituting the optic radiation proceed from the primary centres and end in the visual cortical centre which, as already stated, is localised in the convolution adjoining the calcarine fissure in the posterior part of the occipital lobe. If there are cases of limited destruction of the external geniculate body with consecutive degeneration in the cortex, we will be able to trace more exactly the path of the visual fibres. Such a case is recorded by Henschen; the right geniculate body was completely destroyed and it was found that a great part of the fibres of the optic radiation, especially those occupying the lowest level, were atrophied and could be traced up to the calcarine fissure. It follows from this that the connection between the cortex and the external geniculate body is insured by the fibres of the inferior or ventral portion of the optic radiation. A further proof of the fact that the optic fibres occupy the lower or ventral part of the optic radiation is this: a compression of the superior or dorsal part of the radiation does not cause any visual troubles but a compression of the ventral part results in hemianopsia.



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From the fact that the true visual fibres proceed exclusively from the external geniculate body and end exclusively in the cortex-centre, it does not follow that this region of the cerebral cortex does not exchange fibres with any other basal ganglion than the external geniculate body. In the same way as the visual fibres of the tract end in the external geniculate while other fibres pass into the anterior quadrigeminal body, the cortical centre not only receives all the visual fibres from the external geniculate but also exchanges fibres (probably corticifugal) with the anterior quadrigeminal body. This has been proved by Monakow and others by means of the degeneration method, and has been confirmed by the anatomo-clinical researches of Dejerine and Vialet.

To sum up. The visual fibres form a bundle, about 1 cm. thick, located in the lower or inferior part of the optic radiation or corona radiata. Starting exclusively from the external geniculate body to terminate at the calcarine fissure, this bundle is directed from before backwards, passing on at the level of the second temporal convolution and following a straight line from the geniculate to the calcarine fissure; near its end, the bundle curves round the occipital horn and bifurcates to send fibres to the superior and inferior borders of the fissure.

The projection is also proved, not only for the optic nerve and the tract, but for the geniculate body, the bundle of the radiation and the cortex centre. In the geniculate body, the dorsal part corresponds to the upper quadrants of the retina; in the radiation, and in the cortical centre, the fibres are also arranged so as to correspond to the homologous parts of the retina. In fact, the law of topographic homology applies to the whole extent of the visual path.

Gudden was the first who advanced the view that there are in the optic nerve pupillary fibres, i.e., fibres which, proceeding from the retina, convey impulses, not to the primary visual centre of perception, i.e., to the external geniculate body and then to the cortex of the occipital lobe, but to the anterior quadrigeminal body and from this to the nucleus of origin of the third nerve. The stimulation of this centre determines pupillary reaction by reflex action.

Bernheimer, examining monkeys, has been able to follow a bundle of fibres which becomes separated from the tract before the latter reaches the external geniculate body, penetrates into the white substance of the anterior quadrigeminal body and then extends, by an arched path, to the level of the aqueduct of Sylvius and ends in the nucleus of the third pair.

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Although the existence of the pupillary fibres is not accepted by all authorities, there is little doubt that there are in the optic nerve, in addition to the true optic fibres, centripetal fibres, of retinal origin, the function of which is to carry the luminous impression to the anterior quadrigeminal body, and from there to the photo-motor centre in the nucleus of the third pair. The function itself undoubtedly exists and is most probably carried out by special fibres. Besides, the degeneration of the big fibres of the nerve and tract after removal of the anterior quadrigeminal body, observed by Gudden, seems to point to the existence of the pupillary fibres.

**General Survey of the Visual Conductors and Centres and their Interconnections.**

We are now in a position to take a general survey of the visual conductors and centres and of their interconnections.

To be quite complete, we should consider separately: (a) the optic path proper, i.e., the connection between the percipient elements (rods and cones) of the retina and the visual centre in the cortex of the occipital lobe of the brain; (b) the connection between the cortical visual centre of each side of the brain, which is probably secured by the fibres of the corpus callosum; (c) the connection between each visual cortical centre and other cortical centres, such as the centre of visual memory, the centre for the articulation of words; (d) the connection between the cerebral centres (primary centres and cortical centres) with the motor centres of the intra- and extra-ocular muscles.

The first of these four aspects of our present subject is the only one which is fairly well elucidated.

The optic path proper is made of central or macular fibres (constituting the papillo-macular bundle) and of peripheral fibres.

The central fibres proceed from the small ganglionic cells of the macular region of the retina, each of which transmits the impulses received by a single cone. The bundle of such fibres, i.e., the papillo-macular bundle, soon passes to the axis of the nerve and unites with its fellow at the centre of the chiasma; thence it passes *via* the external geniculate body and the optic radiation to the visual centre in the cortex. Though the path of the papillo-macular bundle beyond the chiasma is not definitely elucidated, yet it seems to be proved that there is a macular bundle in the optic radiation and a special macular centre in the visual cortex.

Though the latter (the macular cortical centre) has not been exactly localised, yet there is very little doubt that a

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function as highly specialised as central vision must be governed by a special centre.

A very important point is that concerned with the necessary connection between the two maculæ and the corresponding visual centres, that in the right and that in the left hemisphere of the brain. Here again, we have no direct anatomical proof of such connection but the persistence of central vision in the two eyes in cases of cortical hemianopsia (see page 283) and also the possible conservation of central vision in double hemianopsia, when all that is left of the visual cortex is but a small unilateral island, cannot very well be explained except by the hypothesis that the bundle of fibres proceeding from each macula is split in the chiasma and thus goes to end in both hemispheres.

Though there appears to be a macular chiasma, yet the maculæ do not appear to be divided into two halves (temporal and nasal) which are capable of being separately paralysed. In other words, there are no cases recorded of macular hemianopsia, and this would be explained by the fact that each cortical centre (right and left) innervates the whole of the surface of both maculæ.

Cajal and others have observed the existence of bifurcated fibres in the chiasma, and it is not impossible that these fibres may be the macular ones which are bifurcated in order that they may go to both hemispheres. Yet, up to now, these fibres have chiefly been seen in animals (rabbit) which have two distinct fields with imperfect central vision and no binocular vision.

Fig. 25 shows, in diagrammatic form, the connections of the macula with the visual centres according to Wilbrand. The bundle proceeding from each fovea (the papillo-macular bundle) is split at the centre of the chiasma to form two separate branches, a direct one which goes to the external geniculate body of the same side and a crossed one which goes to the external geniculate body of the other side. It has not been possible up to now to recognise the bundle of macular fibres connecting the geniculate body to the cerebral cortex though, as stated, it is difficult to think that such a specialised function as macular vision is not governed by a definite cortical centre.

Of the peripheral fibres, those proceeding from the nasal half of each retina form what we have termed the crossed bundle of each optic nerve, while those proceeding from the temporal half of each retina form the direct bundle. The fibres of the crossed bundle occupy the internal and inferior part of the optic nerve; the crossed bundle from one retina passes through the lower part of the chiasma where it crosses

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the similar bundle proceeding from the other retina, and the two together, travelling in the inferior part of the tract, end in the external geniculate body. As to the direct bundle, the fibres of the temporal half of the right retina are collected in a bundle occupying the superior and external part of the right optic nerve and the superior part of the chiasma. They pass into the tract on the same (right) side where they conserve the dorsal or superior position. A similar arrangement is observed for the direct bundle proceeding from the temporal half of the left retina. It is most probable that the fibres of the direct bundle, as they penetrate into the geniculate body, mix gradually, fibre to fibre, with the crossed bundle so that

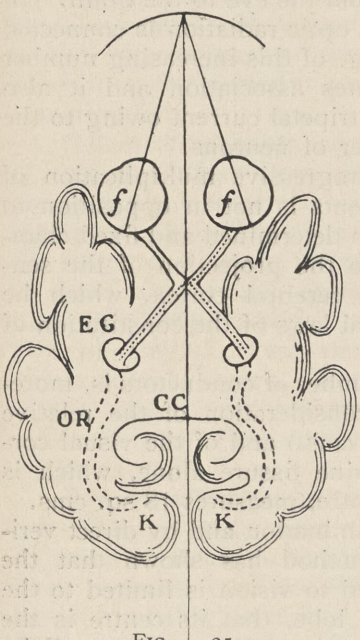


FIG. 25.

FIG. 25. SCHEMATIC REPRESENTATION OF THE CONNECTIONS OF THE MACULÆ AND VISUAL CENTRES. (after Wilbrand).

It should be observed that each fibre of the papillo-macular bundle of the right eye (one of which is shown in dotted lines in the diagram) bifurcates at the centre of the optic chiasma, one branch going to the left external geniculate body EG, the other to the right one. A similar arrangement applies to the papillo-macular bundle of the left eye. The further path of the papillo-macular bundle through the optic radiation OR to the cortex K is not definitely known, though the independent connection of each fovea with both cortical centres is a physiological necessity.

finally there are no distinct bundles but only couples of fibres, each of these couples being made of a direct and a crossed fibre.

This fusion of the bundles does not destroy the projection or topographic homology which seems to be one of the fundamental laws in the constitution of the visual path. In other words, the crossed and direct fibres, now coupled in the geniculate body, still correspond, the dorsal ones to the upper part of the retina, the ventral ones to the lower retinal region. This, at any rate, is rendered probable by clinical facts; for instance, the destruction of the superior part of the

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external geniculate body determines anopsia in the corresponding inferior quadrants of the visual fields.

Beyond the external geniculate body the cylinder-axes proceeding from the cells of this ganglion are united to form the inferior or ventral part of the optic radiation where they form a bundle (visual bundle) of about 1 cm. in thickness and 3 to 4 mms. in width; this bundle, which connects the geniculate body and the cortex, contains a number of fibres greatly exceeding that of the corresponding tract. This multiplication occurs in the geniculate body in which the terminal arborisations of each retinal fibre correspond to several cells; there is, therefore, a progressive increase in the number of cells and fibres from the eye to the brain. In the cortex itself each fibre of the optic radiation is connected with several cells. The advantage of this increasing number of conductors is that it facilitates association and it also increases the intensity of the centripetal current owing to the participation of a greater number of neurons.

According to Cajal, this progressive multiplication of the number of conducting elements is not in opposition to the idea of conductibility through determined and fixed channels. Nor is it in opposition to the projection of the sensorial surface (retina) onto the cerebral cortex, which he regards as one of the fundamental laws of the constitution of the nervous system.

The multiplication in the number of conductors is, moreover, easily explained by the consideration of the relative area of the retina (about 7.5 sq. cms.) and of the visual cortical centre in which the calcarine fissure alone, which is but a small part of the visual centre, measures 18 sq. cms.

Proceeding by successive elimination and by direct verification, the anatomo-clinical method has shown that the part of the cerebral cortex related to vision is limited to the internal surface of the occipital lobe, that its centre is the calcarine fissure and that it extends to the cuneus and the lingual lobe. All this region is characterised by the presence in the cortex of a white substance, formed by a plexus of myeline fibres (optic plexus of Cajal). These fibres are part of the optic radiation, and arborise with star-shaped cells occupying the lower part of the layer of pyramidal cells of the cortex; these star-shaped cells are characteristic elements of the visual cortex and are the probable seat of visual impressions.

Thus, after two centuries, modern researches verify Newton's postulatum and show that certain groups of cells in the cortex receive the impressions proceeding from identical points in the retinæ. In fact, it would be difficult to

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conceive another mechanism for single binocular vision than the reunion, at a single point in the brain, of two fibres emanating from the retinal points in the right and left eyes which receive the same image from outside.

The projection of the retina onto the cortex is most probable in the light of clinical facts and according to Cajal's hypothesis that the sensorial cortical surfaces are the representation of the sensorial peripheral surfaces. The visual cortical centre may be compared to a greatly enlarged retina, folded on itself and onto which, owing to the homology of position of the receiving and conducting elements, the images formed on the ocular retina are projected. If there is a cortical projection of the retina, there must be, *a fortiori*, a macular centre. Henschen thinks that this centre is located at the anterior part of the calcarine fissure; other authors place it at the posterior part; this question requires further investigation.

There is probably no special centre for the perception of colours distinct from the visual centre proper, but there are certainly memory centres for certain kinds of visual perceptions. Cases have been recorded of subjects who could see letters and words without these conveying any meaning to their mind. Such cases prove that "to see" and "to understand what is seen" are two different things, two functions of cerebral organs, distinct and differently located. The visual cortical centre, the position of which we have determined, only presides to what we might call unconscious vision; it is to its association with other centres that conscious vision is due.

The visual cortex is not an organ having a single function like the retina, but a mixed organ including motor elements in addition to its elements for perception. The large pyramidal cells of the deep layer, the cylinder-axes of which probably terminate in the anterior quadrigeminal body, serve to produce the reflex ocular movements, these involuntary movements occurring as the consequence of visual impressions. It has been proved that the stimulation of the visual cortex determines ocular movements most probably by direct action on the elements just mentioned.

Fig. 26 gives a diagrammatic representation of the path of visual impulses. The left half of the diagram shows the optic path from the starting point in the two left retinæ to its termination in the cerebral cortex of the occipital lobe. The right half represents the reflex optico-motor apparatus. The diagram should be carefully studied, as it resumes our knowledge in the matter of the connection of the eyes with the nervous centres.

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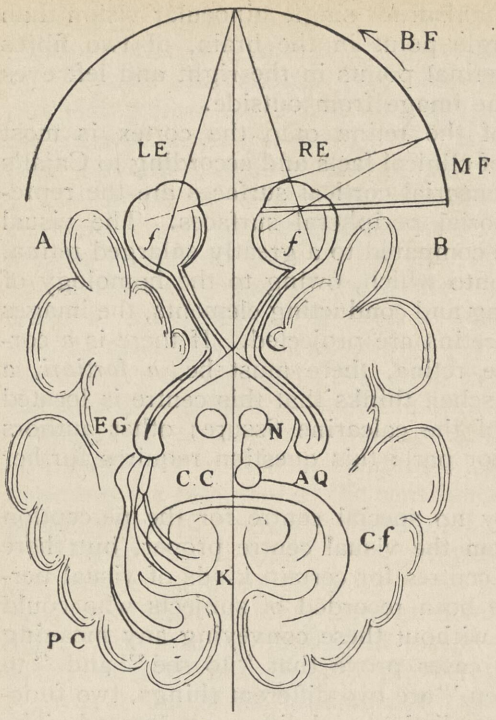


FIG. 26.

FIG. 26. SCHEMATIC DIAGRAM OF THE VISUAL CONDUCTORS. The true visual path is shown on the left half of the diagram. Its constitution results from the respective position of the two eyes with regard to external objects. Thus an object moving in the visual field in the direction of the arrow head forms at first a retinal image on the nasal part of the right retina only, this portion of the retina constituting a zone of monocular vision similar to the whole retina of animals which have their eyes placed so laterally on the two sides of the eye that binocular vision is impossible. The portion of the human retina alluded to just now corresponds to the monocular part M F of the visual field. The bundle of optic nerve fibres proceeding from this portion of the retina crosses in the chiasma (crossed bundle), and has the peculiarity that it does not couple with direct or uncrossed fibres as is the case for the portion of the retinæ corresponding to the binocular field B F. For this reason the crossed bundle is supposed to end in the external geniculate E G of the opposite side, though there is so far no anatomical proof of this fact.

The external object, continuing to move from right to left, enters the binocular part B F of the field. Then its image is formed simultaneously on identical points of the two halves of the retinæ which face to the right. It becomes then a physical necessity, in order that single binocular vision may occur, that the two portions of the retinæ which receive the image of the object be connected with a same point in the cortical centre. It is in this way that the direct bundle must be a new acquisition in animals with true binocular vision; the crossed bundle is, from the phylogenic point of view, the original one. The junction of a direct and the crossed bundle occurs in the external geniculate body. This primary centre is, as we have pointed out, the true primary visual centre from which, according to the data obtained by the degeneration method and the anatomo-clinical method, the fibres of the optic radiation proceed to the cortical centre K in the neighbourhood of the calcarine fissure.

The "pli courbe" (a French term meaning a "curved fold") which is represented at P C in the diagram, is the motor centre for articulated speech.

The reflex optico-motor apparatus is shown on the right half of the diagram. In the right optic tract retinal fibres, which we have called the pupillary fibres, form the centripetal path of retino-motor reflexes. These fibres end in the anterior quadrigeminal body A Q which in its turn is connected with the nucleus of origin N of the third nerve. Corticifugal fibres C f proceeding from the large pyramidal cells of the cortex K end in the anterior quadrigeminal body and are connected with the nucleus N of the third nerve. These fibres serve, no doubt, to the production of reflex movements of cortical origin.

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**Association of the Two Visual Cortical Centres.**

This association is most probably effected by the fibres of the corpus callosum, the commissure or bridge of white nervous matter which connects the two cerebral hemispheres. Though the functions of these fibres are not fully investigated, there is no doubt that they play a part in the association of the reflex movements of the two eyes, when one or the other of the visual cortical centres is stimulated. They also supply a communication between the right visual cortical centre and the associated cortical centre concerned with visual memory which, at least in right-handed people, are only represented in the left hemisphere. Thus, there is a portion of the left cortex, near the fissure of Sylvius, which is termed the centre for visual memory of words and a lesion of which causes the curious trouble called verbal blindness or optical aphasia. Yet, normally, we can read equally well with the right halves of the retinæ which are connected with the right visual cortical centre. It follows that the latter must be connected with the centre for visual memory which is located in the left hemisphere, the corresponding portion of the right hemisphere being untrained for this function. The connection can only take place through the corpus callosum.

The connections between the visual cortical centres and the motor cortical centres which probably occur at the level of the basal ganglia and in the cerebral cortex, are not perfectly known anatomically though their existence is physiologically certain. It is proved that the pupillary fibres of the optic nerve pass into the anterior quadrigeminal body and from it into the nucleus of the third pair.

The motor functions of the cortex have been mentioned above. It is known that the optic radiation contains fibres which do not serve directly to the transmission of visual impressions; these fibres extend from the cortex to the anterior quadrigeminal bodies and constitute motor bundles through which the visual sensations determine certain movements of the body and more especially of the head and eyes.

The fact that the movements of the body, beside depending on the muscular sense, depend also to a certain extent on visual impressions, is shown by the case of subjects affected with tabes dorsalis (or locomotor ataxia), a disease depending upon sclerosis of the posterior columns of the spinal cord. Amongst other symptoms (lightning pains, abolition of spinal reflexes, etc.) tabetic subjects present a loss of muscular sense and are only able to maintain their balance if they keep their eyes open. With their two eyes shut, they sway about and are no longer able to stand upright.

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Let us proceed now with some practical applications of what we have learnt so far on the subject of the path of visual impressions.

It is obvious that any lesion interrupting the course of the optic nerve in its orbital or intracranial part will cause blindness of the eye on the same side. Affections localised to the chiasma or occurring in the immediate neighbourhood of the optic decussation (e.g., tumours, acromegaly, destructive processes in the sella turcica) cause heteronymous defects in the field. (Acromegaly is a disease characterised by general enlargement of the extremities, especially head, feet and hands. It is usually associated with disease of the pituitary body, the hypertrophy of which causes a compression of the chiasma. The sella turcica is a saddle-shaped depression in the body of the sphenoid bone lodging the pituitary body).

Corresponding to the loss of the field on the left temporal or left nasal side, there is a defect of the right field affecting the side of the same name. As already mentioned, the crossed fibres lie in the lower part of the chiasma, the direct fibres in the upper part; hence processes destroying or compressing the upper portion of the chiasma destroy the function of the temporal halves of the retinæ (nasal hemianopsia); processes destroying the lower portion of the chiasma result in a defect of the nasal halves of the retinæ (temporal hemianopsia). The latter form is more common and constitutes what Hirschberg calls "blinker hemianopsia."

A lesion interrupting a visual tract will cause homonymous hemianopsia and we have already spoken of cortical hemianopsia which is also of the homonymous variety. The diagnosis of the seat of the lesion in case of homonymous hemianopsia is based on the pupillary reactions as we shall see presently.

**Visual Troubles Occurring in Hemianopsia.**

Let us first of all study a little more closely the visual troubles due to hemianopsia. It must be clearly understood that left (or right) hemianopsia denotes loss of the left (or right) halves of the visual fields, i.e., anæsthesia of the two half-retinæ looking to the left (or to the right) and therefore situated to the right (or to the left) with respect to a vertical plane passing through the centre of each eyeball.

Hemianopsia may be complete or incomplete, according as the loss of vision bears on the whole extent of the homonymous halves of the fields or only on a portion of these regions. In the latter case, the defect is more often termed

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homonymous hemianopic scotoma; the extent of these scotomata may be small and not exceeding a few degrees, but the essential character of hemianopsia is conserved, namely, however small the size of the scotoma is, it occupies symmetrical positions in the two fields, i.e., regions which coincide in the binocular field.

Hemianopsia may be absolute or relative; it is absolute if the visual function is entirely lost in the affected part; relative, if vision is only reduced (hemiamblyopia) or again if there is only loss of colour vision, in which case, the defect is termed hemiachromatopsia.

In complete homonymous hemianopsia half of the binocular field is lost, that is the portion on the right or the left of a vertical line passing through the point of fixation, but the latter is always in the part of field that is conserved. Central vision is therefore normal, and usually subjects are not aware of the nature of the trouble; in some cases, they are not even aware of the existence of a visual trouble.

If the two visual fields are recorded separately on the usual perimetric forms, it is easy to see that the eye, the temporal field of which is lost, presents a greater deficiency than that of the eye which is deprived of its nasal field; the former has lost 90° along the horizontal, the latter 60° or about so. This is a consequence of the distribution of the crossed and direct bundles; the former (ancestral bundle) innervates about the internal two-thirds of the retina, the latter (acquired bundle) the external third of the retina. With respect to the field, the eye opposite to the lesion is therefore more affected than that on the same side. It is probably for this reason that hemianopic subjects generally refer the visual trouble only to the eye the temporal field of which is lost, that is to the eye opposite to the lesion, exactly as an animal with panoramic vision and deprived of his left visual centre would only be conscious of the blindness of his right eye.

The line of separation of the lost part of the field from the part that is conserved is of importance; this line is generally a vertical one directed through the point of fixation, the latter being always included in the part of the field that is conserved, whether the hemianopsia is right or left. In other words, when the visual field is taken separately for each eye and is recorded in the usual way, it is found that from a point 5° to 10° above to a point 5° to 10° below the fixation centre, the line of separation between the lost field and the conserved field follows a half-circular or half-elliptical path, so that in the horizontal meridian it reaches a point 5° to 10° from the fixation centre towards the lost field. There are individual differences in this respect which are attributed

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to anatomical differences in the relative proportion of the crossed and the direct fibres. It is clear that this conservation of central vision in a case of hemianopsia is necessarily due to a special innervation of the macular region. Each macula, as we have already stated, must be connected with both cortical centres, since the destruction of one of these centres has no effect whatever on the maculæ.

In most cases of homonymous hemianopsia central vision is not affected. All the visual functions are normal in the portion of field that is conserved; the light sense and the limits of colour perception are not modified. Up to quite recently, it was thought that all luminous perception (coloured or not) was abolished in the blind half of the field. Dr. Bard, of Geneva, has found it is not so, that hemianopic subjects conserve a certain amount of light perception in the lost field, and that coloured light is not recognised as colour but merely as light. So far, there is no anatomical interpretation of these facts.

Incomplete hemianopsia is occasionally observed in the form of homonymous anopsic quadrants. Such cases are generally cases of complete hemianopsia which, after a time, have become reduced to the actual condition. The lost quadrants generally extend to the periphery; the apex is a few degrees from the fixation point which, as in a case of complete hemianopsia, is left in the part of the field that is conserved. The acuity is generally normal and the symptoms the subject complains of depend on the portion of field that is lost; for instance, an individual in whom the left upper quadrant in the field of each eye is lost would say that while reading he cannot see the top left corner of his book. It may happen that, instead of two homonymous halves of the fields being lost, scotomata of various size and position may occur. If they always occupy symmetrical positions on the same side of the fixation point in the recorded field of each eye, they are termed hemianopic scotomata, their hemianopic nature being due to the fact that they represent the retinal anæsthesia produced by a unilateral lesion of the cortex or of the optic conductors, a lesion which reacts on homonymous parts of the field owing to the chiasmatic semi-decussation. These scotomata may be paracentral (i.e. near the point of fixation) and cause a certain amount of trouble in almost central vision, or they may be peripheral and hardly perceived by the subject.

The subjective visual troubles occurring in hemianopsia are not always well marked. Subjects may be hemianopic without knowing it, but often they are conscious of some visual disturbance. The hemianope, when looking straight

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in front, is only able to see objects lying to one side, a state of affairs which restricts his free movements in the streets or in open places. This is particularly noticeable if he walks along that side of the street opposite the defect in his field. Reading is difficult, the print appears dull and is badly seen either on the right or on the left of the point of fixation. The fact that the words following that which occupies the point of fixation are not seen is most troublesome in reading and is frequently mentioned by observant subjects affected with right hemianopsia. It will readily be seen that while right hemianopsia greatly restricts the power of reading and writing, the hindrance is not so great in left hemianopsia. Hirschberg relates a striking instance of this in a Rabbi who was affected with right hemianopsia and who was unable to read an English or German text but could read Hebrew without a hitch (Hebrew is read from right to left).

When any of the above symptoms occur, a perimetric examination is necessary. It must be understood that the subject is generally not aware of the binocular nature of his affection; as a rule, he refers it to the eye the temporal field of which is lost. For instance, a patient who does not see on the right thinks his right eye is defective; this is due to the fact that most people are not aware of the part taken by the left eye in vision to the right and conversely.

Hallucinations in the blind part of the field are frequently observed; more rarely in the seeing part. Subjects see faces or animals in their blind fields. Most of them are aware of the hallucinatory nature of these perceptions. These hallucinations have been observed as a symptom preceding hemianopsia. They have, according to Uhthoff, a localising value, as they are more common in cases where the occipital lobe or its immediate vicinity is affected.

Lateral homonymous hemianopsia may be caused by all lesions interesting the optic path from the chiasma to the cortical centre. Thus, we have basal hemianopsia (due to some lesion in the tract), sub-cortical hemianopsia (basal ganglia and optic radiation) and cortical hemianopsia (cortex centre). Up to recently it was thought that the difference between the cortical and the other forms of hemianopsia was based on whether the line of demarcation passed through the point of fixation or not. This difference is now regarded as due to individual anatomical dispositions and, as far as perimetric delimitation is concerned, all varieties of hemianopsia are identical. It is by the study of phenomena associated with hemianopsia, especially the pupillary reactions, that we can acquire important, if not always decisive, information as to the seat of the lesion.

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**The Pupillary Reaction following a Lesion or a Break at a point in the Visual Path.**

We have seen that there are in the optic nerve and tract fibres constituting the centripetal path of the pupillary motor apparatus and ending in the anterior quadrigeminal body. It follows that a lesion of the optic path in front of the anterior quadrigeminal body must alter the pupillary reaction whereas a lesion in the optic radiation or in the cortex has no effect on this reaction. In fact, in the majority of cases of hemianopsia and even of double hemianopsia or cortical blindness, the pupils act normally unless the condition is associated with some lesion of the nucleus of the third pair, and this normal reaction occurs whether the sensitive or the blind half of the retina is illuminated. Wilbrand and Wernicke, guided by the conception of the pupillary fibres, think that in those cases of non-cortical hemianopsia in which the lesion lies in front of the anterior quadrigeminal body (or in front of the point at which the optic path gives off the fibres that go to the oculo-motor nucleus) the pupil only reacts to illumination of the sensitive half of the retina whereas it does not react to illumination of the blind half (hemianopic reaction of Wernicke).

In this research of the pupillary reaction considerable difficulty is experienced and, owing to this, many authorities discount the practical importance of this test. Is it possible to localise the illumination of the retina in order to be sure that the seeing half will not be affected by the light directed on the blind half? It is evidently easy to form on the retina a sharp image of a flame by means of a proper system of lenses, but the image must be fairly bright for the pupillary reaction to be well marked; there will then be some diffusion of light (according to the degree of pigmentation) and this diffusion may affect the seeing half. Such is the technical difficulty that many observers regard it as sufficient to explain how rare are the cases in which a clear and well-marked hemianopic reaction is seen. Some authors have thought to utilise the sensations of the patient. If he perceives a luminous sensation when the image of a flame is formed on the blind retinal half, then the production of a pupillary reaction might be attributed to the diffusion of light on the seeing part. If on the contrary, he does not perceive the luminous sensation, the presence or the absence of pupillary reaction will be quite decisive. But the fact discovered by Dr. Bard and mentioned in page 284, namely, the persistence of luminous sensation in the blind part of the field, complicates the question.

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From all the observations published up to now, it seems that the hemianopic pupillary reaction is a rare phenomenon, but its existence cannot be denied, and if it is possible, in a given case of hemianopsia, to observe clearly hemianopic immobility or even only hemianopic sluggishness of the pupil the fact may be regarded as evidence of basilar hemianopsia. But the absence of this reaction (i.e., conservation of the pupillary reaction for the whole retina) cannot justify the rejection of the diagnosis of basilar hemianopsia for the reason stated above (possible diffusion of light especially in little pigmented eyes).

Some well recorded observations are interesting. In a case described by Samelsohn, there was no absolute hemianopsia but only hemiachromatopsia; the post-mortem examination showed a glio-sarcoma of the tract which compressed the fibres without destroying them; the radiation and the cortex were normal. In another case recorded by Leyden, that of an old woman suffering from left hemiplegia with left ptosis and deviation of the eyes to the right, there was a left hemianopsia with well-marked hemianopic pupillary reaction; the pupils only contracted when the left half of either retina was illuminated. During life, the lesion was supposed to be in front of the anterior quadrigeminal body and the post-mortem showed a softening in the region of the right cerebral peduncle extending to the visual tract on the same side. Hemiplegia is often associated with hemianopsia of basilar origin. The same lesion which compresses or destroys the tract may act on the cerebral peduncle and cause hemiplegia which is crossed with respect to the lesion and therefore situated on the same side as the blind half of the visual field.

We have seen above that the external geniculate body is the only true basal centre containing visual fibres and it follows that only a lesion of this ganglion may cause hemianopsia. It may happen, however, that hemorrhages of the pulvinar compress the geniculate and cause anæsthesia of the superior homonymous quadrants of the two retinæ; i.e., anopsia of the homonymous inferior quadrants of the fields. These troubles are generally temporary and, amongst all the possible lesions of the base, only a complete destruction of the external geniculate can cause persistent hemianopsia.

As we have already stated, the term cortical hemianopsia applies to those cases of hemianopsia due to destruction of the cortical visual centre at the internal surface of the occipital lobe. Lesions of the convex or outside surface of the lobe may cause visual troubles but only if they penetrate

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deep enough to section the optic radiation. As a rule, cortical hemianopsia is rarely found without any other cerebral symptoms. It is often due to arterio-sclerosis which may extend to several arteries and, of course, a tumour may constitute a single localised focus.

To resume what has been said on the subject of hemianopsia. If the continuity of the left optic tract is interrupted at any spot, the left halves of the retinæ would be cut off from their connection with the left cortical centre so that the right half of each visual field would be wanting, or in other words objects situated in the right half of the binocular field would not be seen. The condition is termed right hemianopsia; likewise, an interruption in the continuity of the right optic tract leads to left hemianopsia, i.e., to the suppression of the left half of the binocular field. This type of hemianopsia is called homonymous or lateral. It is termed right or left according as the right or left half of the binocular field is wanting. Such hemianopsia would, of course, occur if the lesion did not affect the optic tract itself, but a spot higher up on the visual path, i.e., the external geniculate body or the optic radiation or even the cerebral cortex. It follows that homonymous or lateral hemianopsia is always indicative of a lesion affecting the central part of the chiasma and upon the same side as the blind halves of the retinæ.

If there is a loss of the pupillary light reflex when light is thrown upon the blinded portion of the retina (Wernicke's hemianopic pupillary reaction, or rather, inaction) the break in the path of conduction must lie below the spot at which the fibres to the oculo-motor nucleus are given off, i.e., it must lie in the optic tract, but if the pupillary light reflex is intact the lesion is to be located higher up; it most often lies to the ventral portion of the internal capsule or still higher in the fibres running from the capsule to the occipital cortex or in the cortex itself. For the reasons stated just now Wernicke's pupillary reaction is difficult to demonstrate, and many authorities contest its value as a means of diagnosis.

A lesion of the chiasma may cause heteronymous hemianopsia. If the chiasma is divided by a sagittal section into a right and a left half, all the decussating fibres are severed, the non-decussating ones being left intact. Since the decussating or crossed fibres innervate the nasal half of each retina, these portions would be thrown out of use and thus the outer or temporal half of each visual field would be suppressed. The form of defect is therefore called bitemporal hemianopsia. It occurs when, as the result of an

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inflammation or of a tumour, the chiasma suffers from a lesion situated mainly in its mesial line and in its lower part. The very rare nasal or binasal hemianopsia in which the nasal half of each field is abolished is caused by a lesion involving the right and left sides of the chiasma especially in the upper part and leaving the central portion intact.

In homonymous hemianopsia it is the rule that the binocular field of vision is not exactly divided in halves, the line of separation bending out a little near the point of fixation so that the conserved portion of the field always includes the macula of each eye. Hence, if there exists a bilateral hemianopsia due to a lesion in both the right and the left cortical centres, the combination of the visual defects on the two sides does not generally give rise to complete blindness but leaves intact, right in the centre, a very small central visual field corresponding to the fovea centralis of each eye.

Hemianopsia in the widest sense of the term exists not only when an entire half of each visual field is lost, but also when there is a deficiency which, though smaller, occupies a symmetrical position in the field of each eye. In such a case there is a lesion of the optic fibres above the chiasma but a portion only of all the fibres of one tract or its continuation to the cortex is destroyed.

**Mind-Blindness.**

Right hemianopsia is often associated, like right hemiplegia, and for the same reason, with various troubles of speech, verbal blindness or optical aphasia, etc. In order to understand this part of our subject, we must bear in mind what has been said (page 81) on the matter of cerebral localisation.

One of the earliest known cases of localisation of function in the cerebral cortex is that of the centre for speech. It was discovered by Broca, who found that patients who had exhibited a curious inability to pronounce definite words or syllables during life were found, after death, to have suffered from disease or injury of the third frontal convolution on the left side of the brain, immediately above Sylvius' fissure. Hence this part of the cortex is called Broca's convolution; the disorder itself is known as aphasia. It may take different forms, from complete inability to speak to an inability to utter certain words and therefore to speak coherently. This centre is, unlike most of the other cortical centres, unilateral, being situated in the left side of the brain.

A subject affected with aphasia in its most typical form, is unable to express himself in words, either spoken or written, and this inability may be of any degree from a



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transient or occasional misuse of a word (such as most people have experienced after hard mental work) to a habitual misuse of words or to their complete loss. The names of persons and of concrete things are the first to go; the verbal symbols of complex and abstract ideas cling closer and longer. Such an affection is termed motor aphasia and its subjects, though possessing ideas, cannot emit them for want of words or emit them in wrong words; "the ideas have no clothes to go out in, or they go out in the wrong clothes" (Waller). It is this form of aphasia which has been found associated with disease of the left third frontal convolution.

The term aphasia is also applied to a form of the disease in which the patient can express ideas in monologue but cannot answer questions, this inability being due to the non-recognition of the words that he hears spoken or sees written. The defect may vary from a transient absent-minded pause, such as occurs in the experience of most people, to the complete blank non-recognition of words. Such an affection is termed sensory aphasia and is also spoken of as word-blindness or word-deafness according as the subject fails to recognise words by sight or by sound. It is found associated with disease of the visual or auditory regions of the cortex, i.e., of the occipital or the temporal regions.

Since Broca, it has been found that in the speech zone there are different centres, centre of auditory images of words, centre of visual images of words, etc. The various forms of motor or sensory aphasia may result from isolated or combined lesions of these centres or from lesions which, though respecting these centres, isolate them from other parts of the brain with which they are normally associated.

A case recorded by Dejerine is most instructive. Man 68 years of age, up to then in good health, has suffered for a few days with numbness and weakness of the right arm and leg. Suddenly he finds he can no longer read a single word, though he distinguishes objects and persons and has no difficulty in speaking and writing. His acuity is 8/10 and he has right hemianopsia. The patient does not recognise letters (literal blindness) or words. To him, A is an easel, S a snake, etc. He can with difficulty recognise a letter by drawing its outline by gesture; the muscular sense awakens the memory of the name of the letter. He can copy a text by drawing the letters (more or less incorrectly) but cannot read what he has written. He can write under dictation, but is unable to find out the mistakes he has made; he prefers to write with his eyes shut as otherwise he is confused. From memory and spontaneously he can write what he likes, but again, he cannot read what he has written.

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Thus, we find in this case right hemianopsia and pure verbal blindness. The power of writing under dictation and spontaneously is conserved. The subject can copy a letter by drawing, but he does not understand what he writes, a symptom which corresponds to verbal blindness. There is also musical blindness; the subject can no longer play at sight. He can read figures and do calculations quite normally. The intelligence is perfect. The condition lasted for four years without modification; then, right hemiplegia occurred, the subject becoming completely aphasic and no longer able to write, though his intelligence was still normal. He died in a coma a few days later.

The post-mortem examination showed: (1) An old softening of the apex of the occipital lobe and of the lingual and fusiform lobes; (2) a focus of recent softening in the postero-inferior part of the parietal lobe. The microscopic examination showed atrophy of the lingual and fusiform lobes; interruption of the internal part of the radiation; destruction of the big longitudinal inferior association bundle.

The first two lesions explain hemianopsia and the destruction of the radiation completes what the cortical lesion might have been unable to do in order to produce complete hemianopsia. The verbal blindness, i.e., the loss of the power of reading and therefore of copying, with conservation of the faculty of writing spontaneously and under dictation, seems to imply an interruption in the path of the fibres associating the visual cortical centre to the centre of the visual memory of words, located in the speech zone. As the anatomical examination shows an interruption in the temporo-occipital association bundle, it is most probable that this bundle is the path of communication between the cortical visual centre and the speech centre.

The subject of visual memory and mind-blindness is one of the most interesting parts of the study of vision. For the successful performance of the function of vision it is essential not only that the eyes should be healthy in structure and function, but also that the brain should co-operate harmoniously in interpreting the impressions made upon the sensory organ. The perfect performance of the visual act may therefore be regarded as the result of the combined and harmonious activity of eye and brain.

The eye is, as we know, an optical instrument so constructed that a picture of the portion of the external world included in the field of vision is thrown upon the layer of the retina constituting the sensorial epithelium (layer of rods and cones). The rays of light striking upon the rods and

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cones set up changes, probably of chemical nature, which give rise to the production of what we have called nervous impulses. These impulses are carried along the visual path (optic nerve, tract, etc.) to a special region of the brain cortex, namely, the occipital lobe, where they are brought into the sphere of consciousness and appear as variations of light, form, and colour.

The optical aspect of vision has long been studied with great attention, but the cerebral or mental aspect of vision had not received the same attention up to comparatively recent years. Yet the brain contributes to each visual act quite as much as the eye itself, and there are many visual defects in which the eye is perfectly healthy and where the lesion lies in the cerebral centres of vision. We should not forget that we see with our brain as well as with our eyes.

The important part the brain takes in the intelligent exercise of vision is clearly shown by the reports we possess of subjects who have been completely blind from birth owing to a congenital cataract and who have been operated upon successfully after reaching maturity.

We borrow the following details from the interesting monograph on "Letter-, Word- and Mind-Blindness," published by Dr. Hinshelwood, of Glasgow. We have to go to the early part of the century for the record of such cases, as we have mentioned just now, since at present subjects with congenital cataract are generally operated upon in infancy. Wilbrand gives an interesting series of such cases. From a study of these it is manifest that vision in our sense of the word was not possessed by these patients immediately after the removal of the opaque lens, which prevented the rays of light from reaching the retina. Even when the operation has been completely successful and clear images of the objects in the external world were thrown on the retina, such retinal images did not at first convey much information to these patients, who had been born blind. The brain had yet to learn to interpret the meaning of these retinal pictures. The patients had to learn by repeated experience and by the confirmation of the other senses, particularly of touch, to distinguish different objects in the field of vision from one another. At first they had no conception of the distance and size of the objects around them. It was only after a time, and by exercising their other senses, particularly touch, that they began to realise the relative size of objects and their relative distances. They gradually learned by repeated experience that the image of an object diminishes with distance and increases with proximity, and thus gradually acquired some idea of perspective. Nor could they at first

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recognise by sight alone the objects which were presented for their inspection. They had yet to acquire a visual memory which, as we shall see, gives us the power of visual recognition. Hence it was only after repeated experience, after they had acquired a sufficiently varied stock of visual memories, that they began to recognise objects by sight alone.

These patients, however, having come to years of maturity, learned to interpret the meaning of their retinal pictures much more rapidly than the child does after birth. They started with fully developed brains, with all their other senses highly educated, and with a knowledge of the external world derived through the medium of their other senses. This sensory knowledge already possessed by them confirmed, corrected, and deepened the impressions of the external world derived from their newly formed visual sense.

The child after birth is much slower in building up his visual knowledge of the external world, because he has as yet no sensory knowledge of it whatever, and all his senses have to be trained simultaneously. It is some time before the infant learns even to fix his gaze on a given object. At first the eye is constantly wandering in restless fashion from object to object and the act of fixation, of directing the eye to a definite object and of keeping it in the field of vision for some length of time, is only gradually acquired by the child. It is only then that clear images of external objects will be fixed sufficiently long upon the retina to enable the higher visual centres in the brain to take cognisance of and register these visual impressions, and thus lay the foundations of that visual memory which, as we shall see, plays such an important part in every visual act. Amongst the first impressions stored in the child's visual memory are the faces of nurse, of parents, and those coming into daily contact with him, and very soon he learns to distinguish them from all others. But it is a considerable time before he acquires any exact knowledge of locality and distance, and if we watch an infant we can see how he gradually elaborates his knowledge of the external world by comparing his visual impressions with the information simultaneously derived through his other senses. The child looks at an object, moves his hands until after several vain efforts he manages to grasp it, then he probably will feel it all over with his hands, may bring it to his mouth, suck it with his lips, or lick it with his tongue. If the movement causes any sound, we can see that the child is taking cognisance of it. The child is thus daily gathering information about the external

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world simultaneously through the medium of all his senses. The ideas of locality, of the relative size and distance of the various objects in our visual fields, are thus gradually elaborated and built up by continuous observation and experience.

The picture of the external world thrown upon the retina is a picture upon a plane surface of two dimensions, and yet the brain has trained itself to translate this into a picture of three dimensions, imparting to it the conception of depth and arranging the different objects in the field at their relative distances from the eye of the observer. The action of the ocular muscles, the degree of contraction or relaxation of the muscle of accommodation, the apparent size of known objects in the field of vision, all these elements combine to enable us to form a correct judgment of the position, size and distance of the different objects in our fields of vision. Such knowledge is only acquired slowly and laboriously by the human being.

In every visual act, therefore, there are complex mental processes involved, and a series of judgments arrived at, before we are able to interpret correctly the picture of the external world thrown upon the retina. But besides the perception of the position, size and distance of the various objects in our field of vision, the brain makes a further contribution by enabling us to recognise the different objects. This is accomplished through the medium of the visual memory, that is, through the power of comparing present visual impressions with the memories of past impressions, which have been preserved in the brain. This aspect of the visual act has met with comparatively little attention nor has it been studied with the care which the great importance of the subject fully merits.

Our senses are not only capable of being acted upon by stimuli from the external world, but the sensations thus produced, if sufficiently vivid and sufficiently prolonged or frequently repeated, leave in the brain permanent impressions, which are preserved and recalled into the sphere of consciousness at the will of the individual. This possibility of preserving and reproducing at will past sensory impressions, commonly called memory, is an essential condition for human progress, otherwise our knowledge of the external world would not increase by prolonged experience of it. But the facts of clinical experience and mental pathology have clearly demonstrated that memory does not exist as a special faculty or unity, but that there do exist individual or local memories, e.g., memories of vision, of hearing, of touch, of taste, of smell, of muscular movements, and so forth; that

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whilst all these forms of memory are intimately connected with each other, yet they are perfectly distinct and independent of each other, so that any single form may be enfeebled, entirely lost or developed to an abnormal extent without any of the other forms exhibiting any corresponding modification. Pathology has further shown that each of these forms of memory occupies a distinct area of the cerebral cortex. Of these special forms of memory, the visual memory contributes a most important factor to every visual act by enabling us to recognise the various objects in our visual field as to their identity, character and qualities.

Schröder has expressed with great clearness certain considerations, which of themselves suggest the improbability of the same sensory cells being the actual seat of visual perception and also of recording and storing up these impressions.

"If the visual perceptive centre in the brain," he says, "is to be relied upon as giving us a true perception of the external world, then the sensory impressions produced in these cells must be pure and unmixed, i.e., must be produced only by the stimuli conducted by the optic nerve fibres from the retina. It is evident that if this same centre and these same cells were employed both in receiving present impressions and in preserving them, that the actual perception would be modified or altered by the voluntary or involuntary activity of the past visual impressions. Further, the visual impressions must remain in this centre only so long as the external stimulus is present, and must disappear immediately after its withdrawal and so render possible the perception of fresh visual impressions. It is thus a necessity that the visual mechanism in the brain must be twofold. It must be able to give us the pure perception of external objects and this perception must remain only so long as it is excited by the stimulus of the external object, but another mechanism must be present, wherein these visual impressions are retained but with diminished intensity, so that they can be readily distinguished from real visual impressions produced by external stimuli, and these impressions or images must be stored up, so that at any future time they can be called into consciousness and compared or contrasted with present visual perceptions."

On purely theoretical grounds, therefore, the argument seems a strong one for the existence of two distinct centres in the brain, a visual perceptive centre, the cells of which are acted upon only by present external sensory stimuli and a visual memory centre, in which are retained the memories of past visual impressions. The facts of clinical experience

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confirm, in the strongest manner, these theoretical views. As to the nature of the impressions received and preserved by the nerve cells in the visual memory centre, we can form no idea. Neither the microscope, nor chemical reagents, nor histology can reveal to us the modifications in the cerebral cells which make possible the retention of past visual impressions, yet consideration of the mental processes involved in vision makes it clear that a visual memory, a storehouse of past visual impressions, has a real existence.

Although every human being endowed with the sense of sight possesses this visual memory, yet it is possessed in very different degrees by different individuals. Some people retain their visual impressions in such a peculiarly vivid way that they can, after long intervals of time, recall and accurately describe the details of a landscape or of a picture, or the peculiarities of a face, almost as if they had it before them. Others possess this power only in a much feebler degree. Francis Galton in his interesting work, "Inquiries into Human Faculty," made a careful investigation into the powers of visual memory possessed by one hundred different individuals, and found the most astounding differences.

Some people in committing a passage to memory do so by means of their visual memory, i.e., when they recall it afterwards, they actually see the words, while others do so by means of their auditory memory and when recalling a quotation, they hear the words. The former have been called "visuels," and the latter "auditives." Galton gives a very good example of a powerful visual memory. He says that he has met with many cases of persons mentally reading off their manuscript, when they were making speeches.

A very remarkable example of vividness of visual memory for form and colour is reported in Dr. Edridge-Green's book on memory and its cultivation. "The following," he says, "was related to Abercrombie by Dr. Duncan, of Edinburgh, who heard it on the spot and saw both pictures. In the church of St. Peter, at Cologne, the altar piece is a large and valuable picture by Rubens, representing the martyrdom of the Apostles. This picture having been carried away by the French in 1805, to the great regret of the inhabitants, a painter of that city undertook to make a copy of it from recollection, and succeeded in doing so in such a manner that the most delicate tints of the original are preserved with the most minute accuracy. The original painting has now been restored but the copy is preserved along with it and even when they are rigidly compared, it is scarcely possible to distinguish the one from the other."

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Horace Vernet, the famous French artist, was said, after looking attentively at an individual for a few minutes, to be able to paint a good portrait of him without ever seeing him again.

These are examples of the great vividness and precision which the visual memory occasionally attains. But though there are very different degrees of retentiveness of visual memory, still every human being endowed with vision possesses it, and makes constant use of it in the recognition and interpretation of the objects which come within his field of vision.

When we recognise a friend in the street, we do so by comparing the present retinal impression with the visual memory of him, which exists preserved in a special area of the brain. When our friend is not present, we can call this visual memory at will into the sphere of consciousness and survey it just as we would an actual picture.

When we recognise a landscape which we have not seen for years, we do so also by comparing the retinal picture of it with the picture in the brain produced by the visual impressions of years ago. When we recognise at a glance the character and uses of all the familiar articles around us, this is also done by comparing the retinal picture with the pictures stored in our visual memory and accumulated by our life experience. In short, whenever the act of recognition of an object falling within the field of vision takes place, this is accomplished by the exercise of the visual memory. It is thus evident what an important part the visual memory plays in each visual act.

We are apt, however, to forget that the intelligent exercise of vision involves such complex cerebral processes, the easy and rapid accomplishment of which is the result of long years of incessant training. The most complicated cerebral processes through continuous practice are carried on with such ease and rapidity that they become transferred to the region of unconscious cerebration. Hence, it is only by a course of reasoning and analysis of the method by which our visual knowledge of the external world is gradually acquired that we arrive at some conception of the processes actually involved. But when disease disturbs the perfect adjustment of the complex cerebral mechanism, it often enables us to catch a glimpse of the processes which are constantly at work in this mysterious region of unconscious cerebration.

We have studied the visual memory by analysing the visual act and by observing the way in which our visual knowledge is slowly and laboriously acquired. In a previous paragraph we have quoted a few typical cases showing how

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disease, interfering with the harmonious working of the complex visual mechanism, produces phenomena at first startling and apparently inexplicable, but a more careful study shows that these phenomena are not only in harmony with our knowledge of the complex processes involved in vision, but throw much additional light on the subject.

There is little doubt now that the cortical centre for optical memory is different from the true visual cortical centre, the latter being located, as we have shown, in the posterior part of the occipital lobe, while the memory centre is in the neighbourhood of the visual centre but not exactly coincident with it, and is located in the left hemisphere, the corresponding part of the right hemisphere remaining untrained for the function considered.

Mind-blindness or psychical blindness may occur in different forms. There may be total mental blindness, in which case the subject does not recognise anything though he sees objects; he is in the condition of a very young infant in whom the retinal images, though perceived by the cortical visual centre, do not determine the ideas or sensations they should normally awaken. From what we have said before, the defect is obviously due to a lack of development or adaptation of the centre for optical memory and the fact that this psychical blindness is occasionally observed is a sure proof that the cortical centre is different from the centre for optical memory. In some cases there may be what is called verbal blindness or alexia, or again, optical aphasia.

In verbal blindness or alexia a written or printed text has no more meaning for the subject than if it were written or printed in a foreign language. The subject may be aware that he sees a text and may turn it the right way if it is shown to him upside down, but occasionally he may not even be able to do that and, in any case, he cannot read it. The trouble may bear on the letters only which are not recognised (literal blindness) or, if the letters are recognised, the faculty of grouping them into syllables and words is lost (syllabic or verbal blindness). The subject may sometimes manage to read by following the outline of the letters with his finger, in which case his muscular sense comes to the rescue. If he has to copy a text, he will do so as if he were drawing it. Reading print may be possible, while music is not, though, in the latter case, the visual memory for letters and words is conserved.

These facts point to the existence of separate memory centres in the neighbourhood of the true psychical visual centre in the posterior part of the occipital lobe in the left

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hemisphere of the brain. Lateral right hemianopsia is generally found in all cases of purely verbal blindness.

In optical aphasia the subject recognises objects, their use and their properties, but has lost the power of naming them. In such cases, the defect is due to some disturbance in the portion of the cortex we have described as Broca's convolution, which is concerned with the production of the movements necessary in articulated speech.

**Association of the Two Eyes in Binocular Vision.**

We shall conclude our study of the nervous apparatus of the eye by a brief investigation of the association of the eyes in binocular vision. The lower vertebrate animals have eyes so laterally placed on the sides of the head that their two visual fields are completely independent without any trace of the overlapping constituting the binocular field

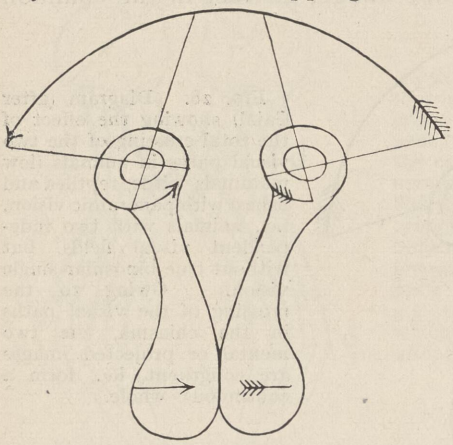

FIG. 27.

FIG. 27. Diagram (after Cajal) to show the lack of congruency which would result from the mental or cerebral projection of the retinal image of the two eyes on the assumption that there is no chiasma, i.e., no crossing, either partial or total, of the two optic paths.

in man and in the higher monkeys. In such animals with separate fields there is no doubt that the right eye sees what is to the right of the median line, the left eye what is to the left, and the field of the right eye is simply juxtaposed to that of the left; this is the kind of vision that has been termed panoramic vision by Cajal. Now, in those animals, the crossing of the optic nerves is complete and we owe to Cajal an explanation of this crossing which, though theoretical is, however, of great interest.

Let us suppose for a moment that there is no chiasma and that the optic nerve of each eye is connected to the optic centre in the brain on the same side (fig. 27). Owing to the inversion caused by the dioptric system of each eye, the two retinal images transmitted to the optic centres are discordant, and it is difficult to see how the brain of the

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animal could reconstruct a continuous impression from the projection of such discordant images.

But really, there is a chiasma, i.e., a crossing of the nerves (fig. 28) which connect the right retina with the left optic centre, and conversely. The lateral inversion is corrected, the two fields continue one another, and the nervous centres receive the impression of the whole object.

In panoramic vision, the total visual field formed by the juxtaposition of the two monocular fields is thus very large, but it is probable that the sensation of relief and depth is rudimentary, if not altogether absent.

In those animals which, owing to the convergence of the visual axes, have a common field, vision gains in quality, especially by the perception of relief, what it loses in extent. The two retinæ instead of receiving images having no common point, receive the same image, at least in the common

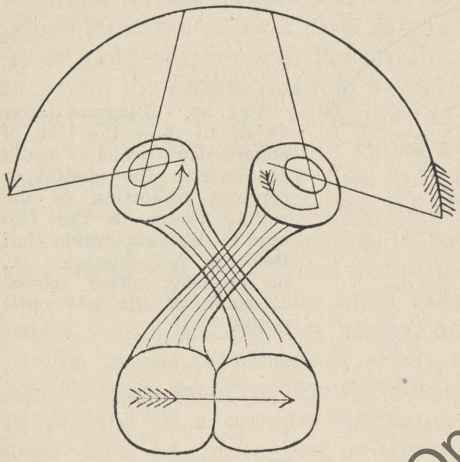

FIG. 28.

FIG. 28. Diagram (after Cajal) showing the effect of the total crossing of the two visual paths in animals (low mammals, birds, reptiles and fishes) with panoramic vision, i.e., animals with two independent visual fields, but without true binocular single vision. Owing to the crossing of the visual paths in the chiasma, the two mental or projected images are congruent, i.e., form a continuous whole.

portion of the two visual fields, the extent to which the two fields overlap increasing with the degree of convergence of the visual axes, as, for instance, from the rabbit to man, passing through the dog, the cat, the horse. At the same time, anatomy shows a direct bundle, very small in the rabbit, very evident in the dog and cat, and more important still in the higher monkeys and in man. The relation between binocular vision and the direct bundle, already mentioned by Newton, is easy to understand by reference to Cajal's diagram (fig. 29).

When the eyes are directed forwards on the same object, it is clear that the homonymous halves of the retinæ (that is the two right halves or the two left halves) receive respectively the image of the same half of the object. In order

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that diplopia may not occur, these two similar images must be transmitted to the same point in the brain when fusion will be produced. By an old ancestral disposition, the nasal half of each retina is connected with the opposite hemisphere; it is therefore necessary that the half of the other retina, which by its relative position is simultaneously impressed (i.e., the temporal half), be also connected with the same hemisphere, thus giving rise to the direct bundle; this bundle will carry to the brain the same part of image as the crossed bundle of the other retina. This is a physiological necessity. How the function has created the organ, by what

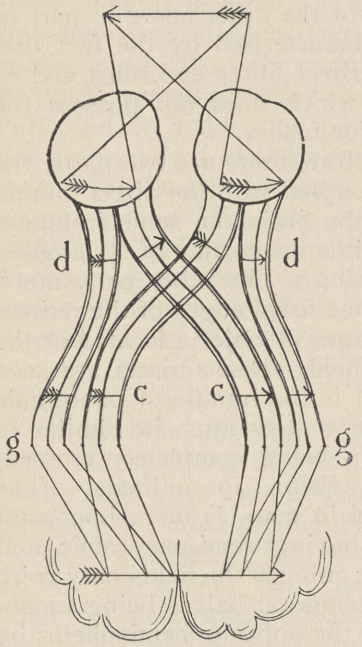


FIG. 29.

FIG. 29. Diagram (after Cajal) showing the formation of a mental image by the synthesis of the projected retinal images transmitted to the cerebral centres by the two optic nerves and tracts in man, and in the higher mammals having a visual field common to the two eyes (i.e., a binocular field). d d represent the uncrossed or direct bundles of the optic nerve; c c the crossed bundles; g g the external geniculate bodies which are connected with the cortical visual centres by the optic radiation.

mechanism a modification in the convergence of the axes has determined the formation of a direct bundle, we are far from knowing at the present time, though the Darwinian explanations are extremely attractive.

In any case, as soon as the homonymous regions of the two retinæ receive the same image, it is necessary that a crossed bundle and a direct one may transport these identical images to the same point of the cortex where they are fused into a single sensation. Hence, a second physiologic necessity in the constitution of the cortex, namely, the existence of cells (termed isodynamic by Cajal) in which the couples

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or groups of optic fibres proceeding from identical points of the retinæ must end. Such is probably the anatomical condition for single binocular vision.

In no vertebrate is the superposition of the two fields complete. Even in man, the sum of the two monocular fields is appreciably larger than the binocular one. (The latter measures 120° horizontally, whereas the sum of the two monocular fields is 200°.) On either side of the binocular field there is, therefore, a zone of about 40° which is seen only by the nasal edge of the corresponding retina. This zone is all that is left, in higher animals and in man, of the panoramic vision of lower vertebrates.

The corresponding bundle of the optic nerve is part of the crossed bundle, but it is characterised by the fact that its fibres are not coupled with direct fibres and must end in a special centre in the cortex which does not possess the histologic disposition required for fusion.

In the crossed bundle, therefore, there are two parts, the more important one, which is coupled with the direct bundle of the opposite eye, carries to the brain the same fragment of images as this direct bundle; it is the portion of the crossed bundle serving to binocular vision. The other part, much smaller, proceeds from the extreme nasal edges of the retinæ, and carries to the brain the images of objects located at the extreme temporal limit of the field; these objects are seen monocularly. This second part is the bundle of panoramic vision; its connections with the centres must be similar to that of the optic nerves, which, being completely crossed, serve to produce panoramic vision in animals. The panoramic bundle, very reduced in man, is more important in those animals (ass, horse) having semi-panoramic and semi-binocular vision. In these animals the fields only coincide by their nasal halves, the temporal halves being monocular and therefore connected to the opposite hemispheres by a crossed bundle not associated with a direct one. If we suppose in such a case a unilateral destruction of the visual path beyond the chiasma, there will be a peculiar hemianopsia in which the lost temporal field (crossed bundle) will be very large and the nasal field (direct bundle) very small.

This inequality of the surfaces of the hemianopic fields is found in man, but to a less extent; the lost temporal field is almost always larger than the nasal field because it includes a binocular part exactly equal to the nasal field and an exterior border corresponding to the extent of the panoramic field. It is to the individual variations of the panoramic field that the relative differences of extent in the blind fields in various cases of hemianopsia are due.

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# CHAPTER XVI.

## THE ORBITAL CAVITY AND ITS CONTENTS. THE EXTRA-OCULAR MUSCLES.

**The Orbits.**

The eyeball lies in the bony orbital cavity of which it only occupies a part, the remaining space being filled with a semi-liquid fat which forms a bed for the eyeball and serves to protect the delicate organ of sight from traumatism.

The skull generally is made up of a number of bones united to each other by sutures which allow no movement to take place, the only exception to this rule being that of the lower maxillary bone or lower jaw which is connected with the rest of the skull by a movable articulation or movable joint. Two distinct parts are recognised in the skull, namely (*a*) the cranial cavity which, as already stated, is in communication with the central canal of the vertebral column, these two cavities being occupied by what we have described as the brain and the spinal cord; (*b*) the face, the bones of which, including the inferior maxillary, are attached to the inferior surface of the anterior half of the cranium, from which they are partially separated by the orbital cavities.

If possible, the reader should have a skull in front of him while studying this portion of our subject, and should handle it so as to gain a clear idea of its structure. All the openings or foramina should be explored by wires so that it may be ascertained into what region they lead. For those readers who cannot have the use of a skull, we have provided two stereoscopic pictures; the first is a photograph of the whole skull (minus the lower maxillary) cut by a vertical plane so as to show the orbits and cavities of the face; the other plate gives a stereoscopic view of one of the orbital cavities taken to a larger scale. (See stereograms I. and II.)

From an actual model, or from the plate referred to just now, it will be seen that the anterior part of the skull includes parts of both cranium and face. Its upper part is formed by the rounded frontal bone. Inferiorly the frontal bone bounds the orbits by the curved supra-orbital margins which are notched towards their medial (nasal) extremities so as to give passage to the supra-orbital nerve and vessels. The notch is called the supra-orbital notch. Each supra-orbital margin terminates temporally at the external angular

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process which meets the malar bone. The medial or nasal extremity of the supra-orbital margin turns downwards to form the internal angular process which meets the lachrymal bone. Between the orbits, the frontal bone articulates with the frontal process of each upper maxillary bone or upper jaw, and with the nasal bones. Above this is a region, the glabella or dacryon, where, in some cases, the remains of the sutures between the two halves of the frontal bone may persist. On either side of the glabella is an elevation known as the supra-ciliary ridge which, during life, is covered by the eyebrows. The most prominent part of the forehead is often termed the frontal eminence.

Below the orbits the face is made up, from the middle line laterally, of the nasal bone, the upper maxillary bone, and the malar, or cheek bone, which forms the prominence of the cheek. In an almost vertical line with the supra-orbital notch, but slightly below the orbital margin, is found the infra-orbital foramen, an aperture giving passage to the vessels and the nerve of the same name. The infra-orbital nerve is a branch of the nerve (7th cranial) which supplies the orbicularis muscle. In the middle line of the face, between the lower halves of the orbits, is the anterior aperture of the nose.

The orbits are situated on each side of the central facial line between the forehead and the face. They are formed of seven different bones, namely, the orbital plate of the frontal bone, the ethmoid, the sphenoid, the lachrymal, the superior maxillary bone, the palate bone and the malar bone or cheek bone. The first three are common to both orbits so that the total number of bones in the two orbits is eleven.

The general shape of the orbits is that of irregular, rounded quadrangular pyramids, the apices of which are extending inwards and backwards. The average width of the orbits in the adult state of man is about 40 to 45 mms., the height 35 mms., and the depth from the free outer margin to the apex about 50 mms. These dimensions are slightly less in woman.

Each orbit has a roof or upper wall, a temporal or external wall, a floor or lower wall and a nasal or internal wall. The angles between these four conventional walls are not well marked but are rounded off, each wall passing gradually and not abruptly into the contiguous one. Owing to this arrangement, it might be more logical to regard each orbital cavity as being irregularly conical rather than pyramidal in shape.

The orbital roof is concave and its surface presents internally a small spine for the insertion of the pulley of the

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superior oblique muscle, and externally a depression for the reception of the lachrymal gland. It is mainly formed by the orbital plate of the frontal bone and, at the posterior part, by a very small portion of the lesser wing of the sphenoid.

The inner wall, from before backwards, is formed by the nasal process of the superior maxillary bone, the lachrymal, the ethmoid, the orbital process of the superior maxillary and the orbital portion of the sphenoid. It is flat and its surface presents the lachrymal groove at its anterior and lower part.

The floor, nearly flat or slightly concave, is formed by the orbital plate of the superior maxillary, the orbital process of the malar and a small part of the palate bone.

The outer wall is formed of the greater wing of the sphenoid and the orbital process of the malar.

The thickness of the outer wall of each orbit varies from 2 to 4 mms., the greater thickness being found posteriorly. The inferior wall or floor is 0.5 to 1 mm. thick and the inner and superior walls are even thinner. It must be observed that the posterior portion of the superior wall is often, in the adult and still more so in elderly people, covered by the frontal sinus which has taken a great development. It follows that the orbital roof is lined, especially on the outside, by the floor of the frontal sinus. In the part of the orbital roof which is not so lined, the thinness is such that this wall is translucent.

Each orbital cavity is in communication with the neighbouring sinuses and with the cranial cavity by nine openings called fissures, foramina, or canals. (In this connection, the term sinus means a cavity in the thickness of some bone.) The most important of these fissures or foramina are: the optic foramen, the sphenoidal fissure, the lachrymal groove and canal, and the spheno-maxillary fissure.

The optic foramen is an oval aperture at the apex of the orbit, through which the optic nerve and the ophthalmic artery pass from the cranial cavity into the orbit. A little below and to the outer side of the foramen we find the sphenoidal fissure, an elongated, irregular slit through which the third, the fourth, the ophthalmic portion of the fifth, and the sixth nerves enter the orbit and the ophthalmic veins leave it. On the inner wall, near its junction with the orbital floor, is the lachrymal groove, followed by the lachrymal canal leading to the nasal cavity. On the lower part of the outer wall there is the spheno-maxillary fissure, through which the middle division of the fifth or trigeminal nerve enters the orbit.



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The projection of the border of the orbit, forming a distinct margin round most of its circumference, results in a diminution of the size of the orbital anterior aperture, the diameter being greater at a little more than two-thirds of the distance from the posterior extremity. The upper border of these orbital arches projects beyond the lower border, permitting a range of vision downwards greater than would exist if the lower border were as prominent as the upper one. Indeed, the whole shape of the orbit is such as to allow a wide range of movement of the globe and a field of view extended in many directions.

In order to allow the eye free movement, the surrounding structures form with it a ball-and-socket joint. The joint cavity is formed by the pouch-shaped structure called the capsule of Tenon. This pouch surrounds the posterior four-fifths of the eyeball; in fact, its folded margin reaches the ocular conjunctiva. It is made of a tough smooth membrane and contains synovial fluid so as to allow the eye the greatest freedom of movement. Since five out of the six muscles which cause the eye movements are attached to the bony wall of the orbit behind and to the front portion of the globe in front (as we shall see more fully presently) it is clear that these muscles, or at any rate their tendons, must necessarily pass through the capsule. This is done in a most admirable way, each tendon taking the capsule with it, so that the fascial cone, extending from muscle to muscle, gives to each a fibrous sheath, thus allowing free movement and at the same time preventing an escape of synovial fluid. Moreover, the edges of the portion of capsule through which the tendon passes give up strong bands which are attached to the orbital edge. These bands act as check ligaments to avoid the possibility of excessive movements of the globe.

The human eye in its normal state is not capable of being moved backwards or forwards, at least to any extent. It simply rotates about a centre of rotation which, considering the ball-and-socket arrangement briefly described just now, could be expected to be at the geometrical centre of the eyeball. Careful measurements by Donders and others have proved this to be the case, and have shown that on an average the centre of rotation is about 13.5 mms. behind the corneal pole in emmetropia, a little less (13 mms.) in hyperopia and a little more (14 to 14.5) in myopia. The possible amount of rotation of the globe in every direction (i.e., the extent of the field of fixation or motor field by contradistinction with the field of vision) amounts to about 88° in the horizontal and 80° in the vertical direction. If the sphericity of the eye is destroyed by disease (e.g.,

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myopia) or if the movements are hampered by an intra-orbital tumour, or again, if there is a partial paralysis of one of the extra-ocular muscles, the amount of rotation is diminished.

We have already stated that, practically, the eye can only rotate about its centre of rotation, but cannot be displaced bodily backwards or forwards or laterally. In animals which have to hunt for their food under bushes (some mammals and a few reptiles) a special muscle, the choanoideus (or funnel-shaped muscle) is inserted on the posterior part of the globe and attached to the back of the orbit. Its contraction pulls the eye backwards into the orbit as a measure of protection. There is no trace of such a muscle, even in a rudimentary state, in the human being. Yet it is a fact of observation that as the result of disease, the globe in man may be pushed forwards (exophthalmia) or sink backwards in the orbit (enophthalmia).

Exophthalmia may be due to an intraorbital tumour, but is more often the result of a disease called exophthalmic goitre, which is characterised by an excessive development of the intraorbital fat.

Enophthalmia is the natural consequence of the emaciation due to prolonged debilitating diseases.

Normally the capsule of Tenon contains muscular fibres which are innervated by sympathetic nerves passing to it via the ciliary or lenticular ganglion. Stimulation of these nerves causes contraction of the muscular fibres, protrusion of the globe and increase in the intraocular pressure. The most important function of these fibres however is, according to Starling, to prevent, owing to their tone, the globe from being dragged backwards into the socket by the action of the recti extra-ocular muscles. One of the explanations of the protrusion of the eye in exophthalmic goitre is given by the same author to be the stimulation of the sympathetic nerves in the neck by the local pressure of the thyroid tumour constituting the goitre. It has been ascertained that removal of the superior cervical ganglion relieves the condition.

As already pointed out, the orbital edge, in the form of a quadrilateral figure with rounded angles, is somewhat narrower than the part one cm. behind it. It follows that a plaster cast of the orbit cannot be removed from the cavity without breaking or cutting the bones.

The projection of the orbital border varies in individuals and races. In all its parts, the orbital edge shows a thickening of the walls; this constitutes the most important defence of the eye against external force, especially

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above, on the external side, and below; the nasal border is not quite so thick; in fact, on the nasal side, there is no sharply defined margin to the orbit, the eye being protected by the bridge of the nose.

The internal wall of the orbit presents at the junction of the lachrymal, superior maxillary and frontal bones, the point we have described under the name of glabella or dacryon, which serves as a starting point for various measurements.

The shape of the orbit varies considerably in individuals, in races and according to sex. Merkel gives for the depth of the orbit an average value of 43 mms. in man and 40 in woman, but he is careful to point out that these figures vary as is the case for all facial measurements. The angle formed by the two orbital axes varies from 40° to 47°; that of the external walls produced, from 87° to 90°; that of the planes of the orbital edges, from 145° to 150°. These data, of small importance in ophthamology, are of interest in anthropology.

The diameter of the base of the orbit is of greater importance in ophthalmology. In this respect, subjects are divided into chamoeprosopes (oval shape of orbital opening) and leptoprosopes (shape of opening tending to become circular). Stilling thinks that if the base of the orbit is low, the superior oblique can more easily exert a pressure on the superior part of the globe, the result of which would be elongation and myopia; hence, chamoeprosopia would be a predisposing cause of myopia. Further researches on this point are necessary.

Beside the possible part of the shape of the orbit in the evolution of defects of refraction, it must be remembered that the orbital index, that is the ratio of the vertical diameter of the orbital aperture to the horizontal one, is of considerable importance in anthropology. The horizontal diameter is a horizontal line from the dacryon; the vertical diameter starts from the point of junction of the malar and maxillary bones on the inferior orbital edge. Before birth, the two diameters are practically equal; as age advances, the horizontal one becomes prominent, more so in man than in woman, and more or less according to races.

To give the index a mathematical value, Broca multiplies the vertical diameter by 100 and divides the product by the horizontal diameter. Thus, in a subject of average height, the vertical diameter being 34 mms., the horizontal one 41.6, the index will be: (100 × 34) ÷ 41.6 or 81.7.

The numerical value of the index varies in individuals and also in races. In subjects with a low index, the orbit is more or less rectangular and has a short vertical diameter;

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in subjects with high index (100 or more) the orbital aperture appears round, especially if the angles are not well marked. The average value of the orbital index is from 90 to 77 in the white race; 95 to 88 in the yellow race; 85 to 79 in the black race.

**Air Cells or Sinuses of the Orbit.**

A few preliminary remarks on the subject of the nasal cavities which are in close proximity to and in communication with the orbit will be useful.

The nasal cavities appear on a skull as two narrow clefts extending between the anterior and posterior nasal apertures and separated from each other by a medial septum partly bony, partly cartilaginous. To examine the structure of these cavities a skull which has been sawn through a sagittal plane should be procured. If this is not available, stereogram I. will be found a good substitute. Parts of both the medial septum and the lateral walls and roof of the nasal cavities are formed by the ethmoid bone. The ethmoid is a very light fragile bone consisting, in part, of the cribriform plate through which the fibres of the olfactory nerve pass. It lies between the two orbital plates of the frontal bone, and its inferior aspect forms the roof of the nasal cavity. Beside the cribriform plate, the ethmoid consists of a thin vertical plate which forms a part of the septum or partition of the nasal cavities and of two lateral masses formed of thin plates of bones bounding numerous air cavities or air cells, to which we shall revert presently. The lateral surfaces of these masses form part of the inner walls of the orbits while their medial surfaces present two or more curled plates of bone, the turbinate bones, under cover of which is a cavity known as a meatus. Each nasal cavity or each nasal fossa is a narrow, vertically placed cavity arched antero-posteriorly so that it is much higher at the centre than at the anterior and posterior ends.

The orbit is surrounded in adult life on three sides by air cells or air sinuses in communication with the nasal cavity. Beneath the floor lies the antrum of Highmore, an air cell in the body of the superior maxillary bone which is present at birth and which in adult life attains a large size. In the roof of the orbit lies the frontal sinus which extends upwards in the vertical plate of the frontal bone; this cell usually begins to develop in the second year of life, and goes on increasing in size by absorption of the bone tissue until old age. The cavity thus formed lies behind the glabella while it extends outwards over the inner two-thirds of the orbit and backwards in its roof for about half-an-inch;

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it is separated from its fellow by a bony septum, usually imperfect, and it communicates with the meatus of the nose by an elongated anterior ethmoidal cell known as the infundibulum. In the lower posterior part of a groove containing the line of the infundibulum opens the antrum of Highmore; this opening, large in the disarticulated skull, is observed to be placed well above the level of the floor of the maxillary sinus. This arrangement allows the discharges of a frontal empyema to find their way readily into the antrum while the opening provided by nature for the passage of air into the antrum forms an unsatisfactory drain for a fluid collection in the same cavity. Moreover, in the articulated skull, the size of the antral opening is much reduced, being overlapped by the vertical plate of the palate.

The cells in the lateral mass of the ethmoid form two groups, an anterior and a posterior one, which are independent of one another. The anterior group opens into the middle meatus of the nose, while the posterior group opens into the superior meatus and sometimes communicates with the sphenoidal air sinus.

The cells of both groups are separated from the orbital cavity by the planum bone (a part of the ethmoid). The lateral mass of this bone shows, when it is disarticulated, many incomplete cells, but in the articulated skull they are completed, in front by the nasal process of the maxillary bone, and the lachrymal bone, below by the maxillary and the orbital process of the palate, behind by the sphenoid, and above by the frontal bone. The lateral mass of the ethmoid begins to be hollowed by air cells in the fourth or fifth year of life, though an indication of the ethmoidal air sinuses can be detected even in foetal life.

The sphenoidal air cells are two in number; they lie side by side in the body of the sphenoid bone; the vertical septum between them is usually imperfect. The lateral wall separates the cell from the apex of the orbit and optic foramen and more posteriorly from the cavernous blood sinus. Above the cells lie the optic chiasma and the sella turcica occupied by the pituitary body. The sphenoidal sinuses are supposed to be an extension from an air cell formed after birth by the folding round of the sphenoidal turbinate bone into a hollow pyramid; the cell invades the body of the true sphenoid about the seventh year. The communication with the nose is by an aperture close to the nasal roof above the superior meatus in the spheno-ethmoidal recess.

Fractures running across the walls which separate any of the above cells from the orbit are likely to be followed by

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emphysema of the retro-ocular tissues and lids, the air leakage occurring in the act of blowing the nose.

The periosteum lining the inside of the orbit is easily detached from the flat bones constituting the walls of the cavity, but at the orbital border it is much more firmly adherent. At the apex of the orbit the periosteum becomes continuous with the dura mater and the dural sheath of the optic nerve.

**Contents of the Orbit.**

Beside the eyeball, the orbit contains a cushion of semi-liquid fat and loose connective tissue which forms the bed in which the eye rotates. It also contains the motor muscles of the eye, the levator of the upper lid, the blood-vessels and nerves supplying the eyes, as well as some vessels and nerves which pass to other parts. The lachrymal gland, the caruncle, the pulley of the superior oblique are also contained in the orbit and Tenon's capsule forms an investment for all these organs.

If the muscles are carefully separated, the optic nerve cut and the eye removed, the cushion on which it rotates appears as a concave hemisphere with a smooth, glistening surface. The lining membrane of this glistening bed is formed by an expansion of Tenon's capsule, which not only serves as a surface on which the eye rests, but which also envelops the muscles, and unites them together, as we will see presently.

The fatty cushion, owing to the conical shape of the orbit and to the extent the eye fills it at the equator, admits of but slight compressibility, and the total displacement of the eye sideways or up and down is not permitted to any appreciable extent.

Normally, there is no important change in the volume of the cushion on which the eye rests and on which it performs its movements. Yet, under certain circumstances of disease or emaciation, the amount of tissue may be appreciably increased or diminished.

**The Capsule of Tenon or Orbito-Muscular Aponeurosis.**

We have already pointed out that the space of the orbit is filled by a fatty material enclosed in a network of loose connective tissue. This fibrous tissue is closely connected with the periosteum, i.e., with the internal lining of the orbital walls, and may be regarded as a modification of this membrane.

In certain places, this fibrous tissue assumes the character of a well defined membrane or fascia which serves as

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an investment of the eyeball and of the tendons of the muscles within the orbit.

The large size and conical shape of the orbit would make it, by itself, a most unsuitable socket for the eye to work in, but really the eyeball comes nowhere in contact with it. It may be regarded rather as a scaffolding for the real socket as well as a store house for the orbital contents. The real socket is the capsule of Tenon in conjunction with its supporting bed of fat supplemented by the concave surface of the eyelids in front.

All the structures contained in the orbit are invested by membranes derived from one and the same aponeurosis; the cornea forms an exception, but it is not, strictly speaking, within the orbit.

The orbital fascia extends from one structure to another, splitting to encapsule each, but it is convenient to commence its study by distinguishing that part which is especially in relation to the ocular muscles.

We have seen that the orbit is of conical shape; the muscles form another cone. Enclosing this cone is a fascial (membranous) cone which extends from muscle to muscle, splitting to invest each with a fibrous capsule. This fascial cone is attached, at the apex of the orbit, to the periosteum round the optic foramen; it widens as it advances in front to be attached to the periosteum all round the orbital margin.

Thus, we have a cone of fascia within a cone of bone, but while the cone of bone contracts at its brim, the fascial

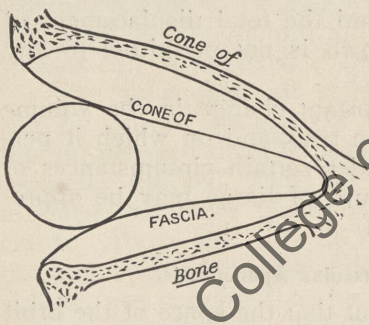


FIG. 30.

FIG. 30. ILLUSTRATING THE ARRANGEMENT OF THE CONE OF FASCIA (FORMED BY THE CAPSULE OF TENON) LINING THE CONE OF BONE FORMED BY THE INTERNAL SURFACE OF THE ORBITAL CAVITY. (after Maddox). While the cone of bone contracts at its brim, the fascial cone expands at its brim, so that a space exists between the two, this space being filled up with the orbital fat, the lachrymal gland, and all the structures located within the orbit. The eyeball is suspended in the fascial cone from above, from below and from all sides. The fascial cone is divided into two chambers (an anterior one for the eyeball and a posterior one for the orbital retro-bulbar fat) by a hemispherical septum or aponeurosis which adapts itself to the shape of the posterior hemisphere of the eyeball. This septum is given off from the main fascial cone about opposite the equator of the globe all round and, from the same line of origin, springs a companion membrane which passes forwards over the anterior hemisphere, investing it closely as far as the sclero-corneal margin, to which it becomes firmly adherent.

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cone expands at its brim, so that an interval exists between the two, and this interval is filled with the periocular fat, the lachrymal gland, etc.

Fig. 30 shows how the eyeball is suspended in this cone, from above, from all sides and from below. The fascial cone lodges the globe in front and is divided into two compartments (the anterior one for the eyeball, the posterior one for the orbital retro-bulbar fat) by a hemispherical membrane which adapts itself to the shape of the posterior part of the globe.

This membrane is given up from the fascial cone just opposite the equator of the eye, and from the same line springs a companion membrane which passes over the anterior hemisphere, investing it closely as far as the corneal margin where it is attached.

These two membranes are regarded as forming a single structure, a single capsule (capsule of Tenon). It sends prolongations backwards in the form of a sheath for the optic nerve and for the various vessels and nerves which enter the eye. Besides, each muscle, on meeting the capsule, does not simply pierce it but is invested by it as is a finger in a glove.

The part of the capsule which invests the anterior hemisphere gives up strips of thickened ligaments (check ligaments) which are attached anteriorly to the periosteum of the orbital edge. These ligaments are posteriorly united with the extra-ocular muscles. Their purpose is to limit the movements produced by contraction of the muscles and also to counteract the pull backwards produced by the recti. (fig. 31.)

It has been proved by Merkel that when a check ligament is cut, an excessive rotation of the eye is permitted in the direction of action of the muscle concerned. Motais has further shown that, after section of a ligament, less muscular power is required to produce a given effect on the eye than when the ligament is intact.

According to Maddox, check ligaments have another purpose, namely, that of slowing off the motions of the eye towards their limit, so as to avoid a shock to its contents by sudden arrest of rotation. It is a mechanical fact that when a force acts on a moving body, there is a constant acceleration of velocity unless the resistance increases proportionally. Were it not for the check ligaments, the sudden stop would develop an excessive degree of kinetic energy since that energy, due to the momentum, is proportional not merely to the velocity but to the square of the velocity.

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It must be remarked that the check ligaments are endowed with a fair amount of elasticity, their maximum extensibility reaching (in the case of the internal and external recti ligaments) a value of 10 to 12 mms.

The rotation of the eye under the action of any muscle does not cease because the muscle has attained its maximum contraction. It is proved, by experiments, that the contraction of the internal rectus required for the maximum physiological excursion of the eye is not more than a quarter of the length of the muscle, whereas it is known that striped muscles are generally, in their condition of maximum contraction, shortened by half.

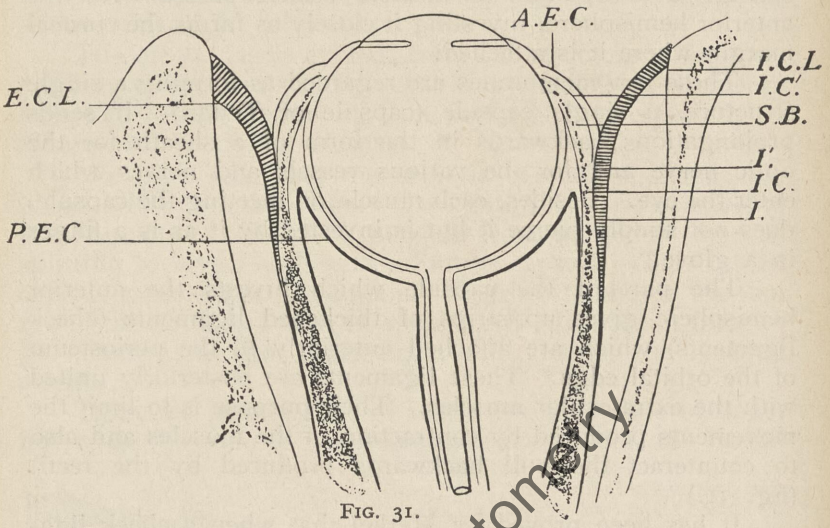


FIG. 31.

FIG. 31. DIAGRAMMATIC HORIZONTAL SECTION OF THE GLOBE AND ITS MEMBRANES (after Motais).

*A.E.C.* and *P.E.C.* represent the anterior and posterior portions of the external ocular capsule or capsule of Tenon; *I, I', I.C., I.C'.* indicate the reflection of the internal capsule over the tendon of the internal rectus. *E.C.L.* and *I.C.L.* are the check ligaments of the external and internal recti respectively.

All the ocular muscles except the superior oblique are provided with something like check ligaments.

**The Ocular Muscles.**

Ocular movements are performed through the action of six ribbon-like muscles, four recti and two obliques.

Except for the inferior oblique they all proceed from the optic foramen; there, the orbital periosteum forms at the apex of the orbit a strong fibrous ring (ring of Zinn) which surrounds and forms a channel for the passage of the

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optic nerve, while it affords an unyielding support for the tendinous origin of the five long muscles as well as for that of the levator of the upper lid.

From this point the five muscles having their origin on the ring of Zinn extend forwards in a diverging direction till they pass the equator of the eye to the places where the four recti are inserted on the globe, while the superior oblique proceeds towards its pulley somewhat in front of the equator, on the nasal side.

At about 8 to 10 mms. from Zinn's ring, the tendons become changed into muscles. They again become tendinous before reaching their insertions on the globe.

**Internal Rectus.**

Besides its origin on the ring of Zinn, it has a tendinous attachment on the sheath of the optic nerve. It passes forwards, nearly parallel to the inner wall, comes in contact with the globe at the equator, and is inserted on the sclerotic about 6 mms. behind the corneal border; the insertion is generally in a straight line or slightly curved with the convexity forwards. It is the largest and strongest muscle: 41 mms. long (Volkman); weight, 0.75 grammes; length of its tendon of insertion, 10 mms.

**External Rectus.**

Is second in strength and third in length. It arises by two fasciculi, one from Zinn's ring (the inferior one), the other (superior one) from the fibrous sheath of the 3rd nerve. It passes forwards, almost parallel to the outer wall, rounds the globe at the equator, and is inserted on the sclerotic about 7 mms. from the corneal border. Length, 40.5 mms.; weight, 0.7 grammes; the insertion on the sclerotic is practically straight.

**Superior Rectus.**

Is the weakest of the four recti; it originates at the upper and outer part of Zinn's ring and at the border of the sphenoidal fissure. Traversing the long diameter of the orbit, it passes round the globe and is inserted 7.6 mms. above and behind the corneal edge. Its length is about 41 mms. and its weight 0.5 grammes. Its tendinous insertion is longer than that of the other recti (10 to 11 mms.) and its line of insertion more curved. The capsular sheath of the superior rectus is so closely united to that of the levator of the upper lid that the action of the two muscles is in a measure associated.

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**Inferior Rectus.**

Arises from Zinn's ring by a tendon in common with that of the internal rectus. It proceeds forwards and is inserted on the sclerotic 6.5 mms. from the corneal edge. Length, 40 mms.; weight, 0.7 grammes. The curved line of insertion of the inferior rectus is so arranged that the vertical meridian of the eyeball would divide this insertion into two unequal parts, the greater being on the nasal side.

**Superior Oblique.**

Arises from Zinn's ring between the origin of the internal and that of the superior recti. The muscle proceeds forwards and inwards towards the superior and internal angle of the orbit, where it becomes transformed into a round tendon passing through the pulley or trochlea. This pulley (fibrous extension of the periosteum) is situated at the trochlear fossa of the frontal bone. From the trochlea, the muscle changes its direction, going outwards, backwards and downwards (forming an angle of 50° with its former direction) expanding into a band which passes upon the surface of the globe between the globe itself and the superior rectus and becomes inserted on the upper, outer and posterior quadrant; the line of insertion is oblique.

**Inferior Oblique.**

Arises from a slight depression in the orbital plate of the superior maxillary bone, at the inferior and internal angle of the orbit, just within the border. Its course is backwards and outwards, passing between the floor of the orbit and the inferior rectus to become inserted by a broad band on the superior, external and posterior quadrant (nearly facing the insertion of the superior oblique).

The insertion of the tendons of the extra-ocular muscles is by no means uniform; the values given above are average numbers and apply to the normal adult eye.

It does not always happen that the lines of insertion of the internal and external recti are so placed as to be perpendicular to the horizontal meridian; this only occurs in about 50 per cent. of eyes. In the other cases, the upper end of the internal rectus insertion approaches more nearly to the cornea and the contrary occurs for the external rectus.

The inner side of the insertion of the superior and inferior recti is usually nearer to the cornea.

In their relation to the horizontal meridian, the insertions of the internal and external recti also vary by being placed more to one or the other side of the meridian line. Thus, in about 50 per cent. of eyes only does the middle

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point of the insertion coincide with the meridian line. When it is not so, the middle of the insertion of the internal rectus is generally below the meridian line, even, in some cases, to such an extent that two-thirds of the insertion is below the horizontal meridian while in the external rectus the greater part of the insertion is above the horizontal meridian. The importance of these variations is obvious. If the irregularity is at all extreme, it may cause a modification in the declination of the vertical meridian. The comparative distance of the insertion from the corneal border will also affect the action of the muscle; the nearer the insertion to the cornea, the greater the influence of the muscle in rotating the eye.

The study of the attachments of the individual muscles to the eye is of great importance to the surgeon, since the extent and direction of these insertions has an important bearing upon the rotation whether by the action of a single muscle or by the united action of more than one.

Fuchs has made a careful and valuable study of the subject. The following is an extract from his table, giving the distance in millimetres of the insertion from the corneal border :—

| MUSCLES. | EMMETROPIA. | MYOPIA. | HYPEROPIA. |
|---|---|---|---|
| Internal rectus ... | 5·5 | 5·5 | 5·2 |
| Inferior rectus ... | 6.5 | 6.9 | 6.0 |
| External rectus ... | 6.9 | 6.9 | 6.4 |
| Superior rectus ... | 7·7 | 7·7 | 7.1 |

As we have pointed out, each of the extra-ocular muscles except the superior oblique is provided with what we have termed a check ligament.

**Check Ligaments.**

The check ligament of the external rectus is a thick band of tissue leaving the external rectus near its anterior extremity, proceeding forwards and slightly outwards to the outer orbital margin. The mean breadth of this band is 7 to 8 mms.; the length between the insertion on the orbital edge and the point of attachment to the muscle is 18 to 20 mms., while the maximum thickness varies from 3 to 6 mms.

The internal check ligament is broader and thinner than that of the external rectus. Its breadth is from 8 to 10 mms.; its length from the attachment to the muscle to the insertion on the orbital edge is 15 to 18 mms. According to Panas, it is more or less fused, by an expansion which covers Horner's muscle, with the internal palpebral ligament so

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that when the internal rectus contracts, it draws back the inner commissure of the lids and the caruncle, pressing at the same time on the lachrymal sac.

For the superior rectus there are two check ligaments. Since the broad tendon of the levator palpebrae is interposed between the superior rectus and the orbital edge, the superior check ligament could not reach the orbital edge without either piercing the tendon of the levator or passing round it. This is the explanation of the existence of two ligaments termed internal and external superior check ligaments. The former is a fibrous cord leaving the inner border of the muscle and following the tendon of the superior oblique to become inserted at the trochlea. The latter is a more flattened band proceeding from the outer border of the muscle and dividing into two branches, one of which joins the check ligament of the external, while the other is attached to the orbital margin in the ordinary way.

The check ligament of the inferior rectus is also double. Beginning at the point where the muscle curves round the globe, it proceeds to the middle part of the inferior oblique, splitting into two so as to embrace it. Then, one of the branches, a slender one, goes to the eyelid; the other is fused with the check ligament of the inferior oblique. The connection with the eyelid explains why the inferior lid is drawn down during contraction of the inferior rectus.

The check ligament of the inferior oblique leaves the muscle 8 to 10 mms. from its insertion on the floor of the orbit, and proceeds obliquely outwards and forwards. It then divides into two branches, one of which goes to the inferior internal angle of the orbit, the other being fused with the ligament of the inferior rectus. The union of this ligament with that of the inferior rectus forms a support to the inferior oblique, somewhat similar to a pulley. By this, we mean that when the muscle contracts the ligament bends the muscle by drawing its middle part outwards so as to make the traction on the eye a little less oblique.

As already stated, the superior oblique has no check ligament.

**Movements of the Capsule of Tenon.**

A glance at fig. 31 shows that between the inner lamina of Tenon's capsule and the sclerotic there is a space (Tenon's space) which represents the arachnoidal space of the eye, since the inner capsule represents the arachnoidal membrane of the brain, and the outer capsule the dura mater. These periocular membranes are indeed continuous with the

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arachnoidal and dural envelopes of the brain though the continuity cannot always be demonstrated.

The capsule, being fixed to the eye at the corneal margin and at the entrance of the optic nerve, accompanies the ocular movements to a great extent, but not entirely, however, except just in front, for its elasticity allows it to give at some places more than at others.

Motais has shown by careful experiments that the fatty tissue which immediately surrounds the eye also, to a large extent, accompanies its movements and each succeeding layer moves less than the one within it. He points out from this that the case of the eye differs entirely from that of a bony socket like the acetabulum, since the capsule and the periocular fat accompany the ocular movements. He suggests that the real socket is the inside of the eyelids since they move least in accordance with its motions. The fact of the matter, as Maddox remarks, is that the eye is an organ *sui generis,* and must not be too closely compared to a bony joint.

The fact that the capsule follows the movements of the eye is of the greatest importance from the point of view of fitting artificial eyes.

**Nerve Supply of the Motor Apparatus of the Eye and of the Contents of the Orbit Generally.**

The subject of ocular movements and of binocular vision belongs to the portion of ophthalmic science called physiologic optics, but a few remarks on the anatomical details concerned with the nervous mechanism of the movements of the eye and with the innervation of the orbit and its contents generally may be useful at the present stage.

The nerves of the orbit are very numerous. They comprise five cranial nerves, namely, the second or optic nerve, the third oculo-motor, the fourth or trochlear, the ophthalmic branch of the fifth or trigeminal, the sixth or abducens, the seventh or facial, and sympathetic filaments to which we shall revert presently.

The optic nerve has been described in full detail (see page 216). Of the other orbital nerves, the third, the fourth and the sixth are purely motor and innervate the extra-ocular muscles. The fifth (trigeminal) is mainly sensory, and the seventh or facial, though it is not a true motor nerve of the eye, inasmuch as it does not take any part in the rotation of the globe, is chiefly concerned with the movements of the lids, and with the working of the superficial muscles in the skin of the face. The sympathetic nerves intervene in the

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movement of the iris and, through the smooth fibres of Müller's muscle, serve to give their tone to the lids.

The innervation of the ocular muscles is accomplished by the third, fourth and sixth nerves. The third (oculo-motor) supplies all the extra-ocular muscles, except the superior oblique and the external rectus, and also innervates the levator of the upper lid, the sphincter of the iris and the ciliary muscle. The fourth (trochlear) innervates the superior oblique, and the sixth (abducens) the external rectus.

The real origins or the nuclei of these three nerves are small masses of grey matter in the lower part of the brain, i.e., in the bulbo-protuberential part, on the floor of the fourth ventricle.

The nucleus of origin of the third or oculo-motor nerve is a small mass of grey matter about one centimetre long lying under the anterior quadrigeminal bodies. Attempts have been made to describe in this mass various secondary nuclei corresponding to each of the muscles innervated by the nerve in question. There is no doubt that such a division seems to be a physiological necessity but, up to the present, anatomy has only shown the main lines of it.

According to Bernheimer, the whole of the nucleus of the third nerve may be regarded as being made of several groups of nervous cells or ganglia, an arrangement which, physiologically, amounts to regarding the nucleus of the third nerve as made of a number of partial nuclei. These partial nuclei are grouped near the median line of the brain and not only are distinct from each other, but each has its own system of vascularisation or blood supply, a fact which explains that a particular vascular lesion does not generally affect all the partial nuclei and therefore does not react on all the muscles innervated by the third nerve.

The portion of nucleus governing the intraocular muscles (i.e., presiding to the pupillary contraction and to accommodation) is near the median plane of the brain, the one belonging to the right hemisphere being practically in juxtaposition with that of the left hemisphere. This would explain the bilateral association of these centres and their association to one another. It is a well-known fact that accommodation as well as pupillary contraction is always bilateral and also that accommodation is always accompanied by a pupillary contraction.

Besides the partial nucleus we have alluded to just now, there are, in the nucleus of the third nerve, three other partial nuclei on either side of the median line, these nuclei

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forming the right and left main lateral nuclei. Fibres proceed from these lateral nuclei as well as from the more median nuclei; the collection of these fibres proceeding from the partial nuclei of the intraocular muscles as well as those proceeding from the lateral nuclei of the levator palpebrae, the superior rectus and a few of those from the nuclei of the internal rectus and inferior oblique run to the eye of the same side, the remaining fibres from the latter two nuclei and all the fibres from the portion of the nucleus governing the inferior rectus run to the eye of the opposite side.

The nervous threads proceeding from the nuclei of origin and forming the third nerve are distinct from each other at their apparent origin on the lower surface of the brain and may be affected separately; they soon join to form the trunk of the nerve; this finds its way through the subarachnoidal spaces of the brain, perforates the dura mater, passes into the external wall of the cavernous sinus together with the fourth nerve, and enters the orbit by the internal portion of the sphenoidal fissure. It is at this stage that the nerve bifurcates and gives rise to a superior branch (which passes into the muscular cone or muscular funnel below the optic nerve and divides again into a portion going to the superior rectus and one to the levator palpebrae superioris) and an inferior branch distributed to the internal rectus, the inferior rectus, and the inferior oblique. From the small branch going to the inferior oblique a fine thread diverges to end in the ophthalmic ganglion, to which we shall refer presently.

The trochlear or fourth cranial nerve has its nucleus of origin in the cerebral peduncle and its apparent origin under the posterior quadrigeminal body. From its apparent origin it runs along the lateral face of the peduncle and under the optic tract to pass into the external wall of the cavernous sinus and enters the orbit by the superior and external part of the sphenoidal fissure, i.e., outside Zinn's ring. It then follows the orbital roof, passing above the levator palpebrae, and gains the upper border of the superior oblique into which it penetrates.

The abducens or sixth nerve has its real origin in the protuberance and its apparent origin in the bulbo-protuberential groove, i.e., at a lower point than those marking the apparent origin of the third and fourth nerves. It pierces the dura mater and passes, not through the external wall of the cavernous sinus, but through the cavity of this sinus in which it is bathed in venous blood. It enters the orbit through the ring of Zinn, and penetrates at once into the external rectus.



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The facial or seventh nerve is really a mixed nerve, but we are not concerned with its sensory portion or nerve of Wrisberg. The motor portion of the nerve originates from a nucleus in the bulb, below the floor of the fourth ventricle. The fibres proceeding from this nucleus emerge from the lower part of the bulb and proceed to the orbicularis muscle, as well as to the muscles of the face.

The sympathetic nerve has two nuclei of origin, one in the bulb, the other in the upper part of the spinal cord. The fibres proceeding from the bulbar nucleus reach the eye in two ways, direct fibres passing to the globe along the path of the trigeminal or fifth nerve, while other fibres pass downwards to end in the nucleus in the upper part of the spinal cord. The fibres from the latter nucleus emerge from the cord together with the roots of the upper spinal nerves and apparently end in the ophthalmic (or ciliary) ganglion. This ganglion, in the form of a small mass about 2 mms. long and 1 mm. thick, is in the orbit on the external side of the optic nerve at the junction of its posterior third and its anterior two-thirds. The ganglion is surrounded by the loose orbital fat we have described above.

The ophthalmic ganglion, which must be regarded as being at the same time a cerebro-spinal and a sympathetic centre, emits nervous filaments, the short ciliary nerves (12 to 15 in number), which pierce the globe around the posterior pole.

The other intraocular nerves form a complex system of mixed nerves through which motor, vaso-motor and sensory impulses travel. This system consists of the short ciliary nerves proceeding from the ophthalmic ganglion as stated just now and of the long ciliary nerves (two in number) which spring from the nasal nerve (a branch of the trigeminal or fifth nerve). All these nerves pass into the globe in the region of the posterior pole around the optic nerve. They travel in the suprachoroidal space, between the sclerotic and the choroid, which latter structure they abundantly innervate. At the level of the ciliary body they divide to form a close plexus (the ciliary plexus) from which proceed fibres distributed to the iris (these fibres are motor, vaso-motor and sensory, and are of cerebro-spinal and sympathetic origin) and to the cornea. Round the corneal margin is a new circular plexus, from which 60 to 80 fine nervous threads proceed to be ramified in the corneal substance and continue in the form of perforating bunches (mostly sensory) which pass through Bowman's membrane and end between the cells of the epithelium layer, an arrangement which gives the cornea its exquisite sensibility.

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The ophthalmic division of the trigeminal nerve (fifth nerve) divides into the lachrymal, frontal and nasal nerves before reaching the orbit.

The lachrymal nerve enters the orbital cavity through the outer angle of the sphenoidal fissure and passes along the outer wall of the orbit to be distributed to the lachrymal gland, the conjunctiva and the portion of the skin near the outer canthus. The frontal nerve enters the orbit through the same fissure above the motor muscles and to the inside of the lachrymal nerve. It passes forwards and divides into the supra-orbital nerve whose exit from the orbit is the supra-orbital notch, and the supra-trochlear nerve, which passes over the superior oblique tendon and leaves the orbit a little inside the supra-orbital nerve. The nasal nerve passes between the two heads of the external rectus, crosses the optic nerve beneath the superior rectus and the superior oblique and above the inferior rectus. It leaves the orbit through a foramen in the anterior part of the ethmoid. Its orbital branches are: (a) a long root going to the ciliary ganglion; (b) the two long ciliary nerves which enter the globe on either side of the optic nerve; and (c) the infra-trochlear nerve which passes beneath the superior oblique tendon and leaves the orbit above the internal tarsal ligament, supplying the conjunctiva, the skin in the region of the inner canthus and the lachrymal sac.

The ciliary ganglion, as we have already seen, gives off the short ciliary nerves which enter the globe around the optic nerve. The superior maxillary division of the trigeminal nerve enters the orbit as the infra-orbital nerve through the spheno-maxillary fissure; it passes along the floor and leaves by the infra-orbital foramen.

It is a well-known fact that the human eye regarded as a single organ simply rotates about a fixed or almost fixed centre which corresponds fairly accurately with the geometric centre of the globe, supposed to be spherical. In other words, the arrangement of the globe in the orbit, or more exactly in the fatty cushion filling the posterior part of the orbit, is somewhat similar to a ball-and-socket system or to the system formed by the almost spherical head of the femur (thigh bone) in the hollow cavity of the hip bone. However, a revolving body of the above kind has full freedom of rotation, i.e. can revolve about any three principal or cardinal axes at right angles to each other (say, the vertical, the horizontal or transversal, and the longitudinal axis) and therefore is free to perform rotations about all other axes resolvable into rotations about two or more of the cardinal axes, from which it follows that a body which enjoys three

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degrees of rotational freedom can rotate about as many diameters as are conceivable.

Actual experiments show, on the other hand, that in the case of ocular movements, one degree of freedom, namely, rotation about the longitudinal axis (or visual line) is not possible for an eye starting from the primary position. The only two degrees of freedom retained are those of rotation about the vertical axis and about the horizontal transversal axis, both being supposed to be fixed in the head. It follows that all ocular rotations can only take place about one of the two above axes, or about any diameter situated in the plane containing these two axes.

In other words, the possible rotations of each eye are limited to rotations about all conceivable diameters in one plane, namely, the plane in which the vertical and transversal axes lie. This plane, termed Listing's plane, which necessarily passes through the centre of rotation and corresponds to a coronal section, is fixed in the head and perpendicular to the longitudinal axis about which rotation is denied.

Thus, when the head is kept erect and the eyes look straight in front at a distant object on the horizon, i.e., when the eyes are in the primary position, however complex the movements of an eye may be in glancing from point to point, the ultimate result of these movements is equivalent to a single rotation of the globe about some axis in Listing's plane, provided, of course, that the eye has started from the primary position.

The study of the individual effect of each of the six extra-ocular muscles shows clearly that only the internal or the external rectus acting singly can produce a rotation about an axis (the vertical one) that is included in Listing's plane. All other muscles would, by themselves, produce a certain amount of torsion and therefore cannot act singly without violating Listing's law.

The matter of the movements of the two eyes together is a more complicated one. To use the words of Maddox, "To the best of our knowledge, every innervation of the ocular muscles is conjugate, and it is impossible for a nervous impulse to descend from the brain to the ocular muscles without being equally divided between the two eyes. In consequence of this, the two eyes work together as a single organ."

The centrifugal impulses to the eyeballs answer to the centripetal arrangements of vision. Homonymous halves of the retinæ convey impressions to the visual centre in the occipital lobe of the same side. For instance, an object

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lying in front and to the left of the field throws its images on the right half of each retina. If these images happen to fall on corresponding points, they are blended into one in the right visual centre. In that case, and if attention is drawn to that object, both eyes move equally and simultaneously as a single organ to bring the images on the fovea of each eye, and thus the object is seen in direct vision. Should, as it more frequently happens, the two retinal images be first formed on non-corresponding points, then, simultaneously with the conjugate lateral movement, an adjustment of convergence takes place, also in a conjugate manner, the two movements being compounded into one.

Every muscle must, therefore, have a yoke-fellow in the other eye; for instance, the superior rectus of one eye is associated with the inferior oblique of the other, and the inferior rectus of one with the superior oblique of the other.

In fact it is impossible to cause a movement to be made with one eye without the other moving also, or at least having a tendency to move. These peculiarities of the ocular movements are evidently not due to the muscular apparatus but to the association of the various nervous centres governing muscular action.

The oculo-motor centres belong to two main categories, namely (a) the primary centres which no doubt are the nuclei of origin of the nerves. These nuclei are made of the cellular bodies of neurons, the cylinder-axes of which run in the trunk of the nerve and end in the muscle concerned; (b) the cortical centres which are double and include a posterior portion which corresponds to the true visual centre in the occipital lobe of the brain, and an anterior portion, less exactly localised anatomically, but which is included in the motor area of the cortex, near the second frontal convolution.

The former governs those ocular movements which are connected with purely visual sensations; the latter, those movements which are due to other sensorial impressions. Besides, there are multiple intermediate centres which may be classified into reflex centres, co-ordinating centres and inhibitory centres. The reflex centres are mainly constituted by the anterior quadrigeminal bodies. In these centres end the cylinder-axes of the retinal fibres which articulate with other neurons so that impulses can be carried to the primary centres and thus cause the visual axes to be directed in any particular direction. The posterior quadrigeminal body does not take any direct part in vision, but seems to be a reflex centre reacting to impulses received via the acoustic path.

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The co-ordinating centres answer a double purpose; some co-ordinate the simultaneous movements of the two eyes in binocular vision, while others co-ordinate the movements of the lids and connect ocular movements with the mechanism of equilibrium and general orientation. The co-ordinating centre insuring binocular rotation with parallelism of the visual axes, are two in number, one in the right, one in the left hemisphere. Their exact anatomical location is not definitely known, though their existence is a physiological necessity; most authorities regard them as being in the anterior quadrigeminal bodies. The centre for the co-ordination of the lid movements is probably in the upper part of the protuberance.

As to the centres of general co-ordination connecting the ocular movements with the phenomena of subjective orientation and objective equilibrium, their location is still uncertain; they are necessarily connected with the vestibular apparatus of the ear. Moreover, the cerebellum plays a large part in the function of co-ordination of movements, but the anatomical position of these co-ordinating centres is not definitely known.

Special motor and inhibitory centres for the regulation of the iris movements have been described in the bulb and the upper part of the spinal cord. It is still uncertain whether there is a true inhibitory centre as well as a motor centre, or whether a single centre can act as motor for the muscle it commands and frenator or inhibitory for the antagonistic muscle.

The connection or association of the above centres is most complex, and consists of:—

(*a*) Association between a particular nucleus with its fellow in the other hemisphere. This association is effected by extremely numerous bundles of fibres in the case of the nuclei of the third nerve. The nucleus of the trochlear and that of the abducens on one side have no such communication with the corresponding nuclei on the other side; this might be expected since the fourth and the sixth nerves of one eye have never to act in conjunction with the corresponding nerves of the other eye.

(*b*) Association of cortical centres. The motor centres in one hemisphere are united together and with the true visual centre in the occipital lobe by association fibres. Moreover, the cortical centres of each hemisphere are associated with those of the other hemisphere by commissural fibres passing mostly through the corpus callosum.

The cortical centres for vision (in the occipital lobe) are united with the centre for speech (on the left side) by

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homolateral fibres for the left speech centre, and by commissural fibres for the right speech centre.

(*c*) The association of the cortical centres with the primary centres is effected by fibres the existence of which is proved by physiological observation and by the anatomo-clinical method. These fibres originate from the motor area in the second frontal convolution, and from the true visual centre, and follow the optical radiation to end in the centre for co-ordination of binocular movements, probably the anterior quadrigeminal body. From there they are distributed to all the nuclei of origin of the motor muscles, since they have to act as motor fibres with respect to some muscles and as inhibitory with respect to other muscles. The great majority of the fibres proceeding from the right co-ordinating centre go, however, to the nucleus of the sixth nerve on the right, and to the portion of the nucleus of the third nerve on the left which is connected with the left internal rectus.

In the same way the left co-ordinating centre for binocular vision is linked with the nucleus of the left external, and with that of the right internal rectus.

This shows that the ocular motor fibres are decussated, so that the right hemisphere of the brain governs the left co-ordinating centre, which in its turn sends impulses to the left external and the right internal recti and vice versâ.

(*d*) The association of the intermediate and the peripheral centres is effected by an important bundle, forming a reflex path, which brings to the nuclei of origin of the motor-oculi nerves and to the nucleus of the facial nerve all involuntary impulses (conscious or not) of visual or auditive nature, or originating from the cerebellum, or due to general sensibility.

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## CHAPTER XVII.

### THE PROTECTION OF THE EYE. LIDS. CONJUNCTIVA AND LACHRYMAL APPARATUS. BLOOD SUPPLY OF THE GLOBE AND ITS APPENDAGES.

Certain structures taking no actual part in vision, but serving mainly to the protection of the globe, are known as Ocular Appendages. Of these, the most important are the eyelids, the conjunctiva and the lachrymal apparatus.

**Eyelids.**

The eyelids are two movable skin folds closing the orbit in front and in close proximity with the globe. They protect the eyeball by their closure which occurs automatically, i.e., by reflex action, if a blow or a foreign body threatens it. The upper lid is larger than the lower one, and more freely movable; it is supplied with a special muscle we have already alluded to under the name of levator palpebræ superioris. The space included between the free borders of the open lids is termed the palpebral opening or palpebral fissure. The eye is commonly spoken of as large or small, according to the size of this opening, which resembles an almond in shape; the size of the palpebral fissure has, however, no relation to the size of the eyeball, though it has the greatest influence upon the expression of the individual. The length of the palpebral fissure is usually 28 to 30 mms., its width at the widest part is about 13 mms.

The boundary of the upper lid is formed by a ridge of bone with a muscle underlying the skin. This ridge, the supra-ciliary ridge, is covered with a growth of hairs called the supra-cilia or eyebrows. The purpose of the eyebrows is to prevent the perspiration from flowing onto the ocular surface. The lower lid passes without any line of demarcation into the cheek.

The eyelids consist mainly of a dense tissue or tarsal cartilage which constitutes a sort of internal skeleton. This tarsus is covered externally with ordinary skin and internally by a mucous membrane we shall describe under the heading of palpebral conjunctiva. The skin of the lids differs from that covering the rest of the body by its thinness, its loose attachment to the subjacent part, and the absence of fat. It is covered by fine downy hairs which are provided with small sebaceous glands, and there are also small sweat glands. At the anterior border the hairs are specially differentiated to

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form a protection to the eyeball; the cilia or lashes are strong, short, curved hairs arranged in two or more closely set rows. Their sebaceous follicles, like the cilia themselves, are specially differentiated and are called Zeiss' glands; apart from being larger, they are identical with other sebaceous glands. The sweat glands near the lid margin are also unusually large; they are situated immediately behind the hair follicles, and their ducts open into the ducts of Zeiss' glands or into the hair follicles, and not directly onto the surface of the skin as is the case elsewhere.

The free edge or margin of the lid or intermarginal strip is covered by a stratified epithelium which forms a transition between the skin and the conjunctiva proper. It shows a row of minute openings just visible to the naked eye; these are the orifices of the ducts of the Meibomian glands. The tarsus consists of dense fibrous tissue containing no cartilage cells, so that the term tarsal cartilage is only justified in so far as it defines the consistence of the plate. Embedded in the tarsus are some enormously developed sebaceous glands, the Meibomian glands. They consist of nearly straight tubes, directed vertically, each opening by a single duct on the margin of the lid. The tubes are closed at their ends and present numerous spheroidal projections giving the glands their characteristic appearance. There are from twenty to thirty Meibomian glands in each lid.

The large bundles of the orbicularis muscle occupy the space between the tarsus and the skin; they appear as dots on a transversal section. The main part of the tendon of the levator palpebræ superioris is inserted into the upper border of the tarsus, but an anterior slip passes between the fibres of the orbicularis to be inserted into the skin of the middle of the upper lid; a posterior slip is inserted into the conjunctiva at the upper fornix. There is no muscle in the lower lid corresponding to the levator of the upper lid, but the inferior rectus and the inferior oblique send fibrous strands forward into the lower lid to be attached to the tarsus.

Besides these striped (or voluntary) muscles, there is a layer of unstriped muscle fibres in each lid; they constitute the superior and the inferior tarsal muscles of Müller. The fibres of the upper one arise amongst the striped fibres of the levator, pass down behind it and are inserted into the upper border of the tarsus. The inferior, which is less developed than the other, consists of a few unstriped fibres interwoven with the fibres of the orbicularis and inserted into the tarsus of the lower lid.

Though the subject of the blood supply of the globe generally and of its appendages will be examined more

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fully towards the end of this chapter, we may state at present that the arteries of the upper lid form two main arches, the superior and the inferior; the former lies at the level of the upper border of the tarsus, the latter just above the hair follicles. In the lower lid, there is usually only one arch lying near the free edge. The veins of the lids form two main groups; the pre-tarsal group which passes into the subcutaneous veins and the post-tarsal group which opens into the ophthalmic vein.

The sensory nerve supply of the lids is derived from the trigeminal or fifth nerve. The third nerve supplies the levator palpebræ and the slips together with the strands proceeding from the inferior rectus and the inferior oblique. The seventh pair, the facial, supplies the orbicularis muscle, and the sympathetic, the two muscles of Müller.

**The Conjunctiva.**

The conjunctiva invests the inner surface of the lids and the anterior segment, and thus conjoins the lids and the eyeball, which justifies its name (*con,* together; and *jugare,* to join). It is divided into the palpebral portion, that is the portion forming the inner lining of the lids, and the bulbar or ocular portion which invests the front part of the eyeball. The fold which marks the reflection of the conjunctiva as it passes from the lid to the globe is called the fornix or the fold of transition. When the lids are closed, the conjunctiva forms a closed sac termed the conjunctival sac. The palpebral conjunctiva is closely adherent to the underlying tarsus and, on account of its thinness, the Meibomian glands are seen more or less distinctly through it.

The palpebral conjunctiva is smooth and glistening in young subjects. In older persons it has a velvety appearance, especially on the upper lid; this condition is often spoken of as papillary, but really this appearance is not due to papillæ but to fine folds into which the thickened membrane has been thrown. A truly papillary condition of the conjunctiva is always the result of a chronic irritation.

In the region of transition between the palpebral and the bulbar conjunctiva (i.e., in the upper and the lower fornix) the membrane is in its loosest condition, being thrown into horizontal folds. The lower fornix may be brought to view by pulling down the lower lid, but the upper fornix is not so readily seen unless the upper lid is very strongly everted. It is clear that if the conjunctiva were to pass directly from the lid to the eyeball every movement of the latter would be hampered, as can be seen in cases in

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which the fornix has been destroyed. Hence, the main purpose of the fornix is to ensure free movement of the eyeball.

The bulbar conjunctiva covers the anterior segment of the eyeball, and may be divided into the sclerotical conjunctiva and the corneal conjunctiva. It must be understood that this subdivision is mainly intended for the purpose of description, and that the bulbar conjunctiva invests the whole of the anterior part of the globe and extends over the cornea as well as over the sclerotic, only, its character changes as it passes from the sclerotic to the cornea; this continuity of tissue explains why diseased processes affecting the conjunctiva corresponding to the sclerotic do not stop at the edge of the cornea, but continue over the latter membrane.

The sclerotical part of the conjunctiva is a thin pellicle, very lax and connected with the sclerotic by a thin, scanty areolar tissue termed the episcleral tissue. The fact that it is so loose explains why a comparatively large amount of bulbar conjunctiva can be sacrificed and the gap covered by drawing the adjacent conjunctiva. Around the cornea, however, the conjunctiva becomes thinner, and is closely adjacent to the cornea itself, forming what is called the conjunctival limbus or *limbus conjunctivæ* (limbus, edge). The bulbar conjunctiva presents, like most mucous membranes, a vascular dermis covered by an epithelial tissue which is made of a few layers of cells and contains none of the glands usually found in mucous membranes.

Over the cornea the conjunctiva is reduced to a very few layers of epithelial cells, and is perfectly transparent; it is so intimately adherent to the subjacent cornea that it may be considered as the epithelial layer of the latter.

**The Lachrymal Apparatus.**

The lachrymal apparatus consists of the lachrymal glands and the channels of excretion or lachrymal passages.

The lachrymal glands consist of the superior or orbital gland, the inferior or palpebral gland, and the accessory glands or Krause's glands. The first two are typical racemose glands scarcely differing from the salivary glands. The superior gland, about the shape and size of a small almond, is lodged in the lachrymal fossa, a small hollow in the outer and upper part of the orbital plate of the frontal bone. Ten or twelve ducts pass from it to open upon the surface of the conjunctiva at the outer part of the upper fornix. The inferior gland, much smaller, lies along the ducts of the gland proper, directly beneath the conjunctiva of the fornix and can be brought into view by turning the

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eye downwards and inwards, while the upper lid is strongly everted. The accessory glands, or Krause's glands, are minute simple glands lying immediately below the conjunctival surface between the fornix and the edge of the tarsus. There are about forty of these glands in the upper and eight to ten in the lower fornix. They empty their secretion into the fornix.

The secretion of the lachrymal glands consists of 98.5 per cent. of water with 1.25 per cent. of mineral salts, chiefly sodium chloride, and 0.25 per cent. of albumin.

The lachrymal channels consist of the puncta lachrymalia, the canaliculi, the lachrymal sac and the nasal duct. The puncta lie near the posterior border of the free margins of the lids, about 6 mms. from the inner canthus. Each lid has one punctum and one canaliculus. The punctum is situated upon a slight elevation, the papilla lachrymalia; it is only visible when the lid is slightly everted, since in normal conditions the puncta are in apposition to the eyeball, so that they may be immersed in the lachrymal lake.

Each canaliculus passes from the corresponding punctum into the lachrymal sac. It is first directed vertically for about 2 mms., then horizontally for about 6 to 7 mms. The two canaliculi usually open separately through the outer wall of the lachrymal sac, but occasionally they join together to form a single canal which opens into the sac.

The lachrymal sac lies in a little depression in the lachrymal bone. When distended it is about 16 mms. long in the vertical direction and 5 or 6 mms. wide. At the lower end it narrows just as it opens into the nasal duct.

The nasal duct, varying much in size (12 to 24 mms. long and 3 to 6 mms. in diameter), passes downwards and slightly outwards and backwards, and empties into the lower meatus of the nose.

The mucous membrane lining the lachrymal passages forms, at different places, folds which project in the lumen of the passage. The largest of these folds occurs at the lower orifice of the nasal duct and is called Hassner's valve, though it is not really a valve capable of closing up the duct but merely a fold produced by the obliquity at which the duct passes through the mucous membrane of the nasal cavity.

The proper moistening of the eye is dependent upon the lachrymal gland and the accessory glands. Normally the amount secreted is just enough to keep the eyeball surface moist and is lost by evaporation. Only under reflex irritation, psychical or of peripheral nature, is an excess of fluid secreted, and this is forced into the lachrymal lake by the

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act of blinking (the lids closing from the outer canthus inwards) and from the lake into the nose through the puncta, the canaliculi and the nasal duct.

It must be remembered that sclerosis or dryness of the conjunctiva does not result from the extirpation of the superior and inferior lachrymal glands, the moistening of the eyeball surface by the accessory glands (Krause's glands) and the mucous secretion of the conjunctiva itself being sufficient to prevent it. On the other hand, epiphora does not usually follow the extirpation of the lachrymal sac, except in the presence of psychical or peripheral stimuli causing an excessive amount of secretion. This shows that under normal conditions there is very little lachrymal fluid that enters the nose, secretion and evaporation from the eyeball surface about balancing each other.

A few supplementary remarks on the ocular appendages may be useful. Secure elsewhere within the bony walls of the orbit, the eye is protected in front by the lids, which are able to close rapidly in order to keep out an excess of light or to lessen the effect of sudden mechanical shocks.

According to Exner, the hairs of the eyebrows and eyelashes are much more sensitive than similar structures in other parts of the body. Their importance from the point of view of protection is obvious; the eyelashes are peculiarly adapted to prevent the penetration of dust particles from the air into the conjunctival sac and the hairs of the eyebrows keep the perspiration of the forehead away from the eyes, beside moderating the action of the light rays from above.

The lids close automatically and remain closed during sleep. During waking hours they also shut automatically, i.e., by reflex action, under the influence of external stimuli. Reflex blinking occurs when the retina is stimulated by a sudden illumination or by the rapid approach of some foreign body to the eye, or again by mechanical or chemical stimulation of the trigeminal nerve, as, for instance, by the action of irritating gases or by mechanical contact with the lashes, the conjunctiva or the cornea.

Apart from the effect of accidental stimuli, there is a periodic blinking of the lids which seems to be intended to propel tears over the eyeball surface; this normal blinking, which takes place at the rate of two or three closures per minute, followed by a rapid opening, increases in frequency when the nerves governing the movements of the lids are irritated by cooling or by drying of the corneal and conjunctival surfaces.

In order that the cornea may retain its perfect transparency, it is essential that it should be continually irrigated

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by a thin layer of lachrymal fluid which keeps it clean and prevents it from drying. This is insured by the secretion and the circulation of the lachrymal fluid. The lachrymal secretion is continuous and is estimated to be about three grammes for each eye daily in normal circumstances. This amount increases under the influence of certain stimuli. The fluid spreads from the outer and upper part of the conjunctival sac by capillarity over the whole of the anterior surface of the globe between the palpebral and the bulbar layers of the conjunctiva towards the inner angle, i.e., towards the lachrymal lake, and as already stated, blinking facilitates the propelling of the fluid in the right direction.

Except when the secretion is excessive, as it is in crying, the tears do not pass over the free margin of the lower lid as they are kept back by the layer of fatty matter secreted by the sebaceous glands at the root of the eyelashes. Lachrymal secretion, like the movement of the lids in blinking, is normally a reflex action produced by external stimuli. These may act on the optic nerve (as a sudden bright light) or on the trigeminal nerve (drying by evaporation or by a current of air, chemical irritation by pungent gases or vapours, mechanical stimulation by particles of dust or other foreign bodies).

As has already been observed, when the lachrymal sac is removed the tears seldom or never overflow the edge of the lower lid unless an increase of secretion is artificially induced. Therefore, it is most probable that in normal conditions there is no draining through the channels of excretion, evaporation from the free surface of the eyeball and conjunctival absorption being sufficient to remove the tears, i.e., exactly balancing the secretion of the glands. It is only when the flow of tears exceeds the normal that the fluid collects in the lachrymal lake and passes through the channels to the meatus of the nose.

As we have already pointed out, the lids are closed during sleep, when the upper lid drops by its own weight and the lower lid is but slightly raised by a weak contraction of the orbicularis muscle. The same mechanism applies to the voluntary gentle closing. Winking movements are intended to renew the fluid film on the cornea and bulbar conjunctiva.

A more energetic closure of the lids occurs by reflex action when a strong light suddenly enters the eye, or on the sudden approach of a foreign body, or by contact of a foreign body with the lashes, or by irritation of the cornea and conjunctiva, or again in sneezing.

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This reflex closure of the lids is an important function in affording protection to the eyes. The reflex can be artificially initiated by the stimulation of any of the branches of the ophthalmic or first division of the fifth (trigeminal) nerve. From the nucleus of origin of this nerve fresh fibres take up the impulses to the upper part of the nucleus of the facial (or seventh) nerve on both sides, and from these to the orbicularis. This reflex is one of the last to be abolished by anæsthetics, and is therefore used as a convenient test; it is often called the corneal reflex.

**Blood Supply of the Eyeball Generally. Nutrition of the Eye.**

The eyeball and its appendages are supplied with blood by the ophthalmic branch of the carotid artery, which itself branches from the aorta and supplies the head generally. The ophthalmic artery enters the orbit through the optic foramen and to the outer side of the optic nerve. The ophthalmic vein which collects the venous blood of the eye leaves the orbit by the sphenoidal fissure and empties into the cavernous sinus (page 337). The various branches of the ophthalmic artery may be divided into two main groups, namely, the orbital group which supplies the lachrymal gland, the lids, the supra-orbital region of the head, the forehead and the nose, and the ocular group which supplies the eyeball itself.

All the arteries supplying the eyeball are divided into two separate sets, the retinal set and the ciliary set. These two sets do not anatomose with each other except at the entrance of the optic nerve into the globe.

The retinal set is based upon the distribution of the central artery of the retina, a small branch which arises from the ophthalmic artery a little behind the globe and pierces the nerve 1.5 to 2 cms. from the globe itself. It then runs along the axis of the nerve as we have described in page 219, to appear on the fundus as if emerging from the depression called the physiologic cup, usually on the nasal side of the disc. On the optic disc, slightly in front of the lamina cribosa, the main artery divides into an ascending and a descending artery, each of which again branches into a nasal and a temporal artery, the branching continuing in arborescent fashion. The retinal arteries are end arteries, i.e., they do not anastomose but merely divide into smaller and smaller branches till they reach the size of capillary vessels. If a branch of a retinal artery supplying a certain area becomes blocked (by embolism) that area degenerates on account of the lack of blood supply.

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During fœtal life, the central stem of the artery continues forwards across the vitreous, to the posterior lens surface and is continued in a canal running through the middle of the vitreous called the central canal or the canal of Stilling. This canal remains in the fully formed eye as a lymph channel, the hyaloid artery having disappeared. The central artery of the retina is accompanied by its vein, lying generally to the outer side of the artery on the disc.

The ciliary set of arteries supplies the rest of the eyeball and is subdivided into the posterior and the anterior ciliary arteries.

The posterior arteries derive from the ophthalmic artery and form a number of short twigs coming off independently or as several trunks from the ophthalmic artery, and pierce the eyeball about the optic nerve. They pass through the sclerotic to supply mainly the choroid. As they pierce the sclerotic, a few twigs are given off which anastomose with a few branches from the central artery of the retina. These twigs unite to form an arterial circle about the optic nerve, the arterial circle of Zinn, from which the nerve substance gets a part of its nutrition.

Along with the arteries passing through the sclerotic and going mainly to the choroid (the short ciliary arteries) there are two other branches, the long posterior ciliary arteries, which run between the sclerotic and the choroid, lying in grooves in the former and reaching the root or periphery of the iris where branches deriving from the two vessels unite to form a large arterial circle (the major arterial circle of the iris). From this circle numerous twigs are given off and converge towards the pupil, around which they form the minor arterial circle of the iris.

The posterior ciliary arteries are unaccompanied by veins.

The anterior ciliary arteries (six to eight in number) are seen beneath the ocular conjunctiva of a purplish colour which does not fade under pressure, and disappear from sight near the edge of the cornea. They run along beneath the ocular conjunctiva in the episcleral tissue to near the edge of the cornea where they enter the eye to supply the ciliary body. Just as they pierce the sclerotic they give up small branches which continue to the edge of the cornea and there anastomose with the long posterior vessels to make up the circumcorneal loops from which the cornea derives its nutrition. The anterior arteries are accompanied by veins forming also circumcorneal loops. The palpebral conjunctiva is fed by the palpebral arteries which pierce the tarsal cartilage to reach it. We have pointed out before

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that the retina has its veins. Almost all the venous blood of the entire uveal tract is collected by the veins of the choroid which converge to either one of four centres, one under each rectus muscle. From these centres large veins arise which pierce the sclerotic diagonally and leave the eyeball to empty themselves into the ophthalmic vein. These veins are the venæ vorticosæ. A small part only of the venous blood of the iris and ciliary body leaves the eyeball through the anterior ciliary veins. Of course, the lids and the conjunctiva have their own veins as well as their own arteries.

**Venous Sinuses.**

As a general rule the arrangement of the circulatory apparatus is that we have described in page 91. Arterial blood loaded with nutriment derived from the digestive apparatus is pumped by the heart into the arteries, reaches the capillaries, which permeate most parts of the body, and is brought back into the heart in the condition of venous blood, i.e., loaded with the waste products derived from the oxidation process constantly going on in the tissues. In a general way we find in all organs one or several veins which collect the blood brought to those organs by the corresponding arteries. There is, however, an exception to this rule, this exception consisting in the existence of blood sinuses mainly found in the brain. These sinuses are peculiar in their structure, inasmuch as they are formed by the separation of two layers of the dura mater, or external envelope of the brain. Lining the cleft or space thus formed is a delicate membrane which is continuous with the internal coats of the veins outside the skull. There are several of these sinuses which are generally three-sided in section, though the smaller ones are more or less circular.

The most important one from our present standpoint is the cavernous sinus, a short and wide blood space at the side of the sphenoid and just outside the orbit. It is traversed by numerous fibrous strands which give it the cavernous appearance to which it owes its name. Posteriorly it communicates with the ophthalmic vein which ultimately collects all the venous blood of the eyeball. Enclosed in the lateral wall of the cavernous sinus from above downwards are the third and fourth nerves, together with the ophthalmic branch of the fifth. The sixth nerve and the fibres of the sympathetic proceeding from the ophthalmic ganglion pass through the cavity of the sinus and are thus immersed in venous blood from which they are separated by a fine covering of endothelium.

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**Nutrition of the Eye.**

From what has been said just now, it is clear that the eyeball is richly supplied by blood-vessels which form numerous anastomoses. Some structures, however, notably the transparent optical media (cornea, lens, vitreous body) have no direct blood supply, and therefore depend for their nutrition on the flow of fluid or lymph from neighbouring structures. This fluid is secreted especially by the ciliary body, and is termed the aqueous humour. As we have already pointed out, the chemical composition of the aqueous fluid is water with a small proportion of mineral salts and traces of organic matter, chiefly in the form of albumin.

After secretion, the aqueous fluid leaves the eye in one of three ways: (1) by travelling through the pupil from the posterior into the anterior chamber and then through the spaces of Fontana at the edge of the iris (the filtration angle) into the canal of Schlemm and thence into the ciliary veins; (2) through the crypts in the anterior surface of the iris into the veins of this structure; (3) between the suspensory ligaments of the lens to the anterior surface of the vitreous then down the hyaloid canal to the papilla of the optic nerve and thus out via the lymphatic spaces of the nerve sheath.

We have already alluded to the first two ways, and we have explained that, whatever the fate of the fluid may be, it is clear that the amount secreted must be the same as that which leaves the globe since otherwise there would be a variation in the intraocular pressure. An insufficient pressure would tend to disturb the correct relationship between the internal structures of the eye and at the same time to prevent the proper action of the ciliary muscle in causing accommodation because the suspensory ligament of the lens would already be relaxed. Too great a pressure, on the other hand, will interfere with the proper blood supply of the eye, and also will prevent accommodation because the tension in the choroid will be too great for the ciliary muscle to overcome.

**Lymphatic Spaces of the Eye.**

The lymph passages of the eye, regarded in the broadest way, may be classified into the anterior lymph passages which carry out the aqueous fluid and the posterior lymph passages, to which we shall revert presently.

We have pointed out before that the aqueous fluid leaves the anterior chamber through the meshes of the pectinate ligament, which forms a fine filter that does not permit the transmission of large corpuscular elements such as the blood corpuscles, but only of liquids and very minute corpuscles.

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According to the prevalent views, these latter pass through the spaces of Fontana into Schlemm's canal, which is comparable to a venous circular sinus. Through the latter, therefore, and through the ciliary veins that anastomose with it, by far the greatest part of the lymph leaves the eye.

Since the pectinate ligament is the main channel of outflow for the eye fluids, very serious troubles are produced by its occlusion. The fluid is retained in the eye and increase of tension develops which leads to blindness. Injury to the filter of the pectinate ligament may occur in several ways. There may be occlusion of its minute openings by corpuscular elements which stick fast in them, or by clots; or again, the delicate meshwork of the pectinate ligament may be transformed into a tough and impermeable structure by remains of embryonic tissue or by inflammation, or finally, there may be apposition of tissue, usually the iris, which is applied to the pectinate ligament and thus cuts it off from the cavity of the anterior chamber.

These changes, which form the basis of increase of tension in the human eye, i.e., the production of the condition termed glaucoma, may also be produced artificially, in which case an artificial glaucoma can be set up.

As we have already pointed out, the iris must be regarded as a subsidiary channel of outflow from the anterior chamber. The injection of Indian ink in a state of minute subdivision into the anterior chamber shows that the particles of ink penetrate into the anterior layer of the iris stroma, where they are taken up by the blood-vessels and carried off. The penetration chiefly takes place through the openings in the anterior surface we have described as the crypts of the iris; through these, the tissue of the iris stroma is in free communication with the cavity of the anterior chamber. Clinical observations confirm this fact; when, for instance, after an iridectomy, the anterior chamber is filled with blood this disappears rapidly wherever it lies upon the iris which takes up the blood, while it remains for a longer time upon the capsule of the lens in the area corresponding to the true and to the artificial pupil.

The part played by the iris in carrying off the aqueous fluid is usually regarded as comparatively insignificant; yet according to recent researches it seems that the iris is the part through which most of the aqueous is taken off; moreover, the fluid thus passing into the iris is not discharged into Schlemm's canal, as is the case for the portion of aqueous which filters through the meshes of the pectinate ligament, but it passes into the anterior ciliary veins by way of the lymph spaces in the sheaths of these vessels.

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The posterior lymph passages are the perichoroidal space, i.e., the space between the sclerotic and the true choroid, a space which is occupied by the lax tissue of the suprachoroidal membrane and the lymphatic spaces between the sheaths of the optic nerve. The perichoroidal space is continued outwards along the vessels which pass through the sclerotic, especially the venæ vorticosæ, and thus communicates with Tenon's space which lies between the sclerotic and Tenon's capsule. From this, the lymph reaches the spaces which run between the sheaths of the optic nerve. Besides these, there is assumed to be another lymph passage in the posterior portion of the globe which corresponds to the hyaloid canal in the adult and to the central artery of the vitreous in the embryo. Pathological processes show the existence of such a lymph passage which runs in the vitreous straight back to the head of the optic nerve, for even in slight inflammation of the anterior portion of the eye, the papilla is often found implicated though the posterior part of the globe may otherwise be normal; we must therefore admit that irritant substances from the focus of inflammation can reach the nerve head and the spaces between the sheath of the nerve by a direct channel through the vitreous.

However, the posterior lymph passages carry only a small fraction of the lymph out of the eye and whether there are diseases which are referable to interference with this discharge of lymph is still uncertain.

From these considerations, it results that there must be a proper control of the elimination of lymph in order that the intraocular pressure may be maintained at its normal value.

The study of the regulations of the intraocular pressure is somewhat beyond the scope of the present work. It is sufficient for our purpose to mention the fact that experiments carried out by Henderson have distinctly proved that there is such a regulating mechanism and that as the arterial blood pressure increases or decreases so does the intraocular pressure. While the arterial pressure varies between 70 and 180 mms. of mercury, the intraocular pressure was found to vary from 23 to 40 mms. The change in intraocular pressure is therefore less than one-sixth of that taking place in the blood and it follows that the controlling mechanism must have considerable efficiency.

In normal conditions, the intraocular pressure in the healthy human eye is found to be between 25 and 30 mms. of mercury. The tension thus set up in the eyeball is principally borne by the sclerotic, though to some extent assistance is afforded by the choroid, owing to its elasticity and

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by Tenon's capsule, owing to the tonic contraction of its smooth muscular fibres which are innervated by the sympathetic system.

It is a fact of observation that, though the cornea and the anterior half of the globe have attained their full development about the fifth year, the eyeball as a whole does not reach its full size till about the seventeenth or eighteenth year of life. During the intervening years, the axial growth of the eye takes place solely behind the equator by a process of retrocession of the posterior pole which continues until the eyeball is of the normal physiological length corresponding to emmetropia. Anything that tends to diminish the resisting power of the young and comparatively soft sclerotic will cause an excessive yielding of the unsupported posterior pole before the normal intraocular pressure and so produce an excessive axial length of the globe or, in other words, the condition known as axial myopia. It was thought at one time that axial myopia was due to an increased ocular pressure brought about by an excessive action of the extra-ocular muscles, especially owing to the convergence required to bring the two visual axes to bear on the object looked at, this excessive action being more than the coats of the eyeball could withstand. The Austrian oculist Arlt was in favour of this theory. Yet, if his hypothesis were true, the lamina cribosa, being necessarily the weakest spot in the eyeball wall would be driven backwards as it is in glaucoma, but this never occurs in myopia. The researches of Henderson, to which we have alluded just now, proved that, in normal conditions, the pressure within the eyeball and that within the sheaths of the optic nerve and brain are exactly the same; therefore the lamina cribosa has really no pressure to withstand and so always retains its normal relationship to the adjacent parts of the ocular wall. If, however, the intraocular pressure be raised, as occurs in blocking of the filtration angle, the lamina is pushed back giving rise to the condition known as glaucoma, whereas if the intracranial pressure is raised, as is the case in a brain tumour, the lamina cribosa is pushed forwards, the condition being then known as choked disc. It should be observed that an increase of intraocular pressure occurring in a child when the sclerotic has not reached its full resisting power, will cause a distention of the whole globe and the production of the condition called buphthalmos or infantile glaucoma.

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## CHAPTER XVIII.

### METHODS OF EXAMINATION OF THE LIVING EYE.

Though the purpose of this book is mainly the study of anatomy, yet a few remarks on some of the methods of examination of the living eye may be useful. We do not propose to investigate all the various steps in a complete clinical examination of a given case, but merely to indicate some of the methods whereby details of anatomy can be made out.

The shape of the globe is of importance. It is a well known fact that in high hyperopia there is a marked shortening of the antero-posterior axis, while in high degrees of myopia we have a lengthening of the antero-posterior axis. In either case, the shortening or lengthening is entirely confined to the posterior hemisphere. It follows that no one can, by simple inspection of an eye from the front, say much concerning its refractive condition. But if the subject opens his eye widely, or still better, if the observer separates the lids with his fingers and then directs the subject to look strongly to one side, the equatorial region of the globe is brought into view and in high degrees of refractive error, the alteration in length becomes visible.

The examination of the state of the lid margins, that of the insertion of the cilia, together with the observation of the shape of the anterior segment of the globe and the arrangement of its constituting parts can easily be carried out with the naked eye or a magnifying glass can be used. Though some of the oculists in the first half of the 19th century (e.g., Sansom, Mackenzie, etc.) used a convex lens for the purpose of the examination of the anterior segment of the living eye, Helmholtz must be regarded as the first to make a systematic use of this method of investigation, which he also employed to ascertain the changes occurring during accommodation. Liebreich must have the credit of having introduced the examination by means of a convex lens in actual practice, and Von Graefe pointed out about the same time as Liebreich (1855), the extreme importance of local or focal illumination used in conjunction with a magnifying glass to detect the presence of slight opacities in the refracting media (i.e., the cornea and lens).

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**Corneal Loupes.**

It is well known that a convex lens used as a magnifying glass gives erect, enlarged virtual images of objects lying within the focal length of the lens. An ordinary trial case lens of 15 to 20 D may be used, but certain magnifying instruments of higher power have been devised for the purpose. Thus Nachet's small pocket loupe consists of a cylindrical tube 27 mms. long and 20 mms. diameter with a + 20 D lens at each end. The instrument magnifies about three diameters and has a fairly large field.

Steinheil's loupe consists of a solid piece of glass mounted in a ring. It has a convex surface at each end and is constricted in the middle. The sides are blackened and the constriction, which is also filled with black varnish, acts as a diaphragm and minimises the aberrations which otherwise would be troublesome. The working aperture is 35 mms. and the focal distance practically 20 mms. The image viewed is very clear, and the field sufficiently large, but the instrument is necessarily somewhat heavy.

Hartnack's achromatic and aplanatic loupe consists of a short metallic tube of 20 mms. in length, carrying a series of lenses, the total effect of which is + 60 D. The aperture is 16 mms., and the focal distance the short one of 16.6 mms. The linear magnification is about 5 diameters. The field is fairly large.

Brucke's loupe is perhaps the most satisfactory design for the examination of the cornea and the front part of the lens in the living eye. It consists of two concentric metal tubes, the inner one sliding into the outer one. The instrument is 95 mms. long when the tubes are drawn out and 70 mms. when closed. The object lens is made of two plano-convex lenses of 20 D and 10 D respectively, placed with their flat surfaces turned towards each other and at such a distance that the equivalent focal length is about 35 mms. The eye-piece is a concave lens of 25 D with a diaphragm to minimise the aberrations. In fact, the instrument amounts to a Galilean telescope adapted to view objects at short distances. When the tubes are drawn out the instrument has an equivalent focal length of 48 mms., and magnifies six times. With the tubes closed, the focal distance is 60 mms. and the magnification 4 diameters.

**Corneal Microscope.**

A still better result is obtained by means of a high-power corneal microscope. The latest model of Sutcliffe's Keratometer can be used as an ophthalmic microscope. The

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two boxes containing the doubling apparatus are drawn half way out so that about one and a half inch aperture in the object lens of the telescope may be left without any doubling device. The instrument is thus reduced to a short focus telescope, or more exactly, to a microscope which is focussed on the patient's eye. The instrument may be used either in daylight if the telescope is so placed that the light from a well-illuminated window can fall sideways on the eye under examination, or still better, the special lamps fitted to the stand of the keratometer may be used so that a strong diffused light can be thrown on the eye.

A very beautiful enlarged and inverted image of the lids, the eyelashes, the sclerotic, cornea and iris will be seen. A slight readjustment of the focussing is necessary as one passes from inspection of the lids to the inner parts of the eye. By careful adjustment the deeper parts of the lens can be illuminated.

The keratometer is fitted with two eyepieces, one of low magnification and wide field, the other with a much higher power and smaller field of view. These two eyepieces are mounted in a way similar to the double nose-piece of the ordinary microscope and can be brought in position, one after the other, almost instantly. The magnification varies from about 5 or 6 diameters with the lower power (or longer) eyepiece to 12 or 15 with the higher power (shorter) eyepiece.

As an ordinary magnifying glass is intended for monocular vision, and the same remark applies to the various methods or the various modifications of it we have briefly described just now, these methods do not easily give that

FIG. 32.

FIG. 32. BINOCULAR CORNEAL LOUPE reproduced by kind permission of Messrs. J. & R. Fleming, Ltd.

perception of relief and solidity which is so necessary in the examination of the eye. For this reason, binocular corneal microscopes or binocular corneal loupes have been devised.

A convenient and simple form is the binocular corneal loupe which consists of two sphero-prisms, bases in, placed

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in a frame which can be strapped on the observer's head so as to leave his hands free (fig. 32). A more elaborate model (fig. 33) carries a small electric lamp fixed at the upper part of a frame in which the lenses are mounted and serves to illuminate the portion of the anterior part of the eye under examination.

One of the most satisfactory binocular corneal microscopes is that devised by Czapski, in which binocular vision is obtained by a combination of two short focus telescopes, each of which is made of a convergent object-lens, and a convergent eyepiece; between the object-lens and the eyepiece of each telescope, a system of prisms is inserted, the purpose of which is, as in prismatic binoculars, to permit a

FIG. 33.

FIG. 33. BINOCULAR CORNEAL LOUPE WITH ELECTRIC ATTACHMENT reproduced by kind permission of Messrs. J. & R. Fleming, Ltd.

shortening of the instrument, an erection of the image and a wider field with a good stereoscopic effect. A special mechanical arrangement permits to obtain a variation in the pupillary distance between 56 and 76 mms. The handling of the instrument is extremely simple. The subject is placed with his chin on a fixed chin rest or his forehead applied to a head rest as is done in most modern ophthalmometers and keratometers. The pillar carrying the twin telescopes can be moved forwards or backwards by means of a screw, and the adjustment of the height is obtained in a similar way. A little lamp of 6 volts with a reflector is fitted above the twin microscopes and serves to give a good illumination of the anterior part of the eye.

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**Focal or Oblique Illumination.**

A more complete examination of the anterior segment of the eye requires the use of oblique or focal illumination. The principle of the method consists in creating a strong contrast between the area that is being illuminated and the surrounding area which is kept in darkness.

The principle of focal or oblique illumination is easily understood. When a beam of solar light enters a dark room through a hole in the shutter, the path of the beam is shown by millions of fine particles of atmospheric dust dancing in its course and the beam is thus sharply defined owing to the contrast with the surrounding darkness. If the shutters are open to flood the room with sunlight or even in ordinary diffused daylight, we do not see so readily the particles floating in the atmosphere because they receive light from all directions, and are therefore all equally illuminated; consequently they do not excite any visual sensation since they do not contrast with their surroundings. Such a contrast is a requisite of every sensory perception. In the case of a single sunbeam the particles of atmospheric dust on the path of the beam are intensely illuminated, their minute surfaces reflecting or scattering light like so many mirrors, while those in the surrounding air remain in darkness. A sharp contrast is the result and we are so enabled to see the particles, i.e., the path of the beam, quite easily.

This principle is applied in lateral illumination of the anterior segment of the eye, a method often termed oblique or focal illumination. Though it is impossible to produce such a striking contrast as that obtained in the case of the atmospheric dust in the sunbeam, i.e., intense illumination beside absolute darkness, still a considerable amount of light can be thrown upon some portions of the eye and shade upon the neighbouring area, thus causing a marked contrast. The bright light is obtained in a dark room at or near the apex of a cone of light proceeding from a source (the ordinary light used in ophthalmoscopy or retinoscopy) concentrated on the part of the eye that is being examined by a strong convex lens. The surrounding darkness is likewise due to the lens and is really the shadow of the peripheral portion thrown round the illuminated area, a fact which does not usually receive the consideration it deserves. Of course, the contrast is diminished by diffused light falling from the walls and the various objects in the room, but this does not cause any considerable disturbance.

When it is proposed to examine the details of structure of the anterior part of the eye by focal illumination, it is necessary for the observer to vary the direction of his vision;

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a faint grease spot on a piece of paper is seen more easily if it is looked at slantingly. In the same way, a slight flake of mucus or a faint corneal opacity is more easily recognised if viewed very obliquely. Another reason why we should change the direction of our gaze is that the corneal reflex (i.e., the catoptric corneal image of the source of light) is very disturbing at certain points and is avoided by a proper change of position of the observer's eye. Also, in the examination of the cornea and aqueous fluid, the background of the transparent cornea and aqueous varies as it is formed by the black pupil or the coloured iris, and it is obvious that a slight corneal opacity will be more easily recognised on the black background of the pupil, while a dark foreign body will show more easily on the background formed by a light iris.

It is likewise necessary to alter the direction of the cone of light to perform a complete examination. Generally the axis of the cone of incident light is almost at right angles to the visual line of the subject's eye; hence the term lateral illumination, but to see the lens the incident light has to be more nearly in front of the subject; this might be called perpendicular illumination. To see the changes which may occur in the nucleus and the deep parts of the lens, the axis of the illuminating cone should almost coincide with the visual line.

In practising the ordinary focal or oblique illumination the room should be darkened as much as possible and the walls and ceiling should be of dark colour to avoid reflection at their surfaces. The source of light may be an ordinary electric bulb, or even an incandescent gas burner. In any case, it is well to have the source enclosed in an opaque box or an asbestos chimney fitted with an aperture level with the source and adjustable in size by means of an iris diaphragm. The lens serving to illuminate the part of the eye which is being examined should be a convex one of 15 to 20 D; a weaker lens does not give a sufficient illumination.

The aperture of the lens should be 4 to 4½ cms. Another convex lens of 12 to 20 D or any of the corneal loupes previously described may be used as a magnifying glass.

The observer and the subject should be seated opposite each other, the source of light being 50 to 60 cms. to the side and a little in front of the subject. The observer holds the illuminating lens in a plane perpendicular to the line joining the source and the subject's eye, and from 6 to 8 cms. from the latter. The apex of the cone of light produced by the illuminating lens is then thrown upon the part of the eye which is being examined, or better still, a little

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behind that part so that a bright illuminated circle, surrounded by darkness, be projected on the subject's eye. By slight movements of the hand of the observer which holds the illuminating lens, or by slight movements of the eye and head of the subject, different parts of the anterior segment of the eye are illuminated and can be viewed by the observer, either with the help of a simple magnifying glass (held at a distance from the subject's eye somewhat less than its own focal length) or by means of one of the corneal loupes described above.

**The Slit-Lamp.**

Of recent years, the examination by focal illumination has been rendered much more perfect by means of what is called a slit-lamp, originally devised by Gullstrand and manufactured by Zeiss. The introduction of the slit-lamp has made possible the microscopic examination of the anterior segment of the living eye with a magnification which cannot be obtained by the older methods of investigation. The principle of the slit-lamp is easy to understand. The cornea, the aqueous fluid, the crystalline lens and the vitreous, though transparent, produce by reason of their structure a certain amount of scattering of the light falling upon them. This scattering is sufficient, if the illumination is intense and critical, to render visible the structure of these apparently transparent media.

The function of the slit-lamp illuminator is to produce upon the part under observation an intensely bright and well defined image of an illuminated slit, thus illuminating a portion of the tissues which can readily be examined through the surrounding transparent structures which, not being illuminated, will generally be invisible. The illuminated section will then be seen standing out brightly and contrasting most perfectly with the surrounding background. The area illuminated depends of course upon the width of the slit image and therefore on the width of the slit itself, which is adjustable.

Just as it is obviously important that a section of any tissue viewed under the microscope should be thin, so in order to secure a good resolution of details in the portion of an eye examined by the optical device we are now concerned with, the image of the slit must be narrow and its definition as good as possible. In order to secure this condition it will be seen that it is necessary to keep the observing microscope directed towards the exact focus of the illuminating beam as only at this point will the section be thin and clear cut.

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An excellent form of slit-lamp has been devised by Mr. E. F. Fincham, of the Northampton Institute. In the original slit-lamp of Gullstrand, the illuminating system and the observing microscope were free to move independently; this necessitated the readjustment of both direction and focus when the inspection was moved from one part of the eye to another.

In Fincham's lamp both the illuminating apparatus and the microscope are mounted upon an arc which has its centre at the focus of the illuminating beam. (See fig. 34.) Then the only adjustment that is required is the focussing of the

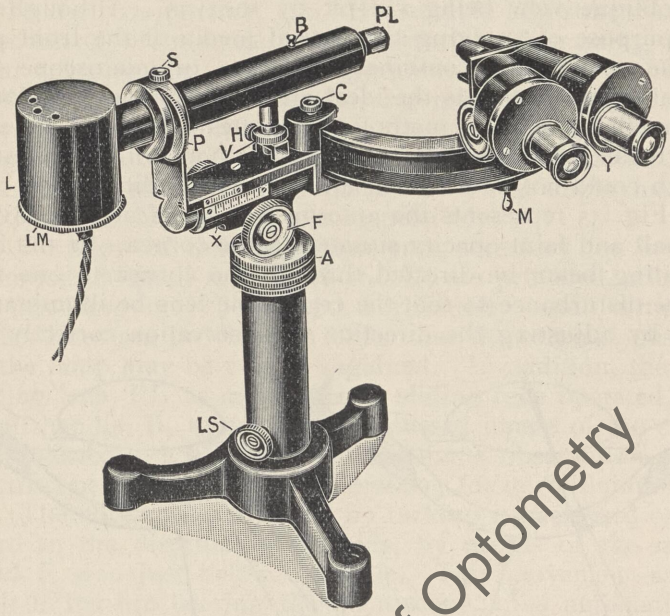


FIG. 34.

FIG. 34. THE FINCHAM SLIT-LAMP. Reproduced by the courtesy of Messrs. Clement Clarke, Ltd.

A is a screw serving to raise or lower the whole instrument. B is the handle of a sliding tube carrying the projecting lens PL; C is a clamping screw to immobilise the arc carrying the microscope; F is the focussing screw of the illuminating part of the instrument. H and V are screws for the horizontal and vertical adjustment of the illuminating part; L is the lamp housing with the lamp mount LM; LS is the locking screw of the pillar; M the handle for rotating the microscope along the arc which carries it. X is a focussing scale and a vernier. Y is a Greenhough binocular microscope which can be replaced, if desired, by a monocular microscope fitted with an erecting prism.

projected image of the slit upon the part of the eye that is to be examined, when the image of the latter will automatically be brought into the centre of the field of the microscope.

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This adjustment is made by racking forward the arc carrying the two components of the instrument, exact focussing being secured when the image appears centrally in the microscopic field. The microscope may then be focussed independently to suit the observer's vision. In order to examine the anterior part of the globe under various angles, it is only necessary to move the microscope along the arc, the centring and focussing remaining unchanged. This movement is necessary as, although where possible it is often desirable to examine the section perpendicularly to the illuminating beam, a smaller angle of observation must be employed when observing the deeper structures, owing to the oblique view being cut off by the iris. Although for the purpose of studying the optical media of the front part of the eyeball the combined centreing of microscope and illuminating system is the ideal arrangement, yet it is found in practice that many pathological states of the eye are seen to greater advantage by indirect methods of illumination which could not be obtained under these conditions.

Fig. 35 represents the anterior portion of an eye having a small and faint opacity situated in the cornea. If the illuminating beam be directed through the cornea to one side of the disturbance so that the crystalline lens be illuminated, then by adjusting the direction of observation correctly the

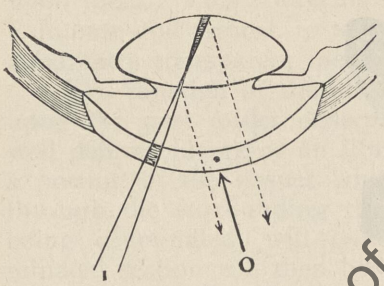


FIG. 35.

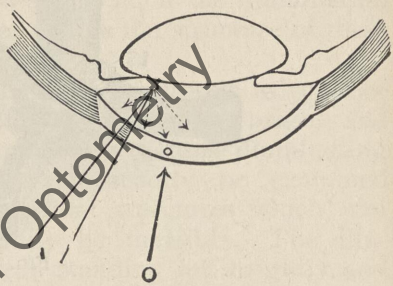


FIG. 36.

I—Illuminating beam. O—Direction of observation.

(Reproduced from the Transactions of the Optical Society).

opacity will be seen more or less dark against the bright background of the lens. Under these conditions the density of the opacity can be estimated by comparing its brightness with that of the background.

It is sometimes possible to illuminate such an opacity, and observe it against a dark background, by arranging the directions of observation and illumination as in fig. 36. In this case the beam is concentrated upon the iris from which, if it be pale in colour, sufficient light is scattered to illuminate

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the small white or translucent body in the cornea. The microscope is then directed so that the opacity illuminated in this manner is seen against the dark background of the pupil.

The optical arrangement of the Fincham slit-lamp is easy to understand from fig. 34. The illumination is produced by a 12-volt Osram gas-filled lamp having a vertical spiral filament. This is found to give a well-defined image sufficiently free from aberration. In the plate P carrying the slit are two circular apertures of different diameters, either of which may be substituted for the slit when it is desired to examine the surface either of the optical media or of the iris, conjunctiva, etc. By suitable adjustment of the direction of illumination and observation when using a circular aperture, the tesselated appearance of the corneal endothelium or even the stellate arrangement of the lens fibres may be made visible. The No. 3 eyepieces of the microscope give a magnification of 19 diameters, and this may be increased to 25 or to 34 diameters by the employment of the No. 4 or No. 5 eyepieces respectively.

To allow of the the adjustments necessary for indirect illumination small screws, H and V, are provided, whereby the slit-lamp may be moved horizontally and vertically. Index lines are provided in order that the original position of the lamp may be readily regained. In addition, the projecting lens, PL, is mounted in a sliding tube operated by a small handle, B, to enable the focussed image of the slit to be projected to a point behind that under observation in the microscope; this condition is necessary for retro-illumination.

The slit-lamp is focussed by racking it backward or forward in the direction of its axis, by means of the milled head F seen just below the scale. This movement carries with it the arc bearing the microscope, thus automatically maintaining the centreing of the two components.

An important use of the slit-lamp is the determination of the apparent depth of the anterior chamber, a measurement of considerable value not only in experimental work but also to the surgeon in the diagnosis of glaucoma. This is made with the existing forms of corneal microscopes by determining the adjustment necessary in order to focus successively the cornea and the anterior surface of the crystalline lens. This method is, however, open to error, as it depends upon the observer's estimation of exact focus and also upon the control of his accommodation. These difficulties are avoided in making the measurement with the slit-lamp. Owing to the fact that the microscope is directed constantly to the focus of the illuminating beam, the observed surface

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will appear central in the microscope field only when the light is accurately focussed upon it. It is therefore only necessary to measure the amount of movement required to bring successively the posterior surface of the cornea and the anterior surface of the lens into coincidence with a central cross wire in the field of the microscope to obtain the apparent distance between these two surfaces. To enable these readings to be taken, a small scale and vernier X have been fitted to the focussing slide of the instrument.

In the latest model of the Fincham slit-lamp, a Greenhough binocular microscope Y is fitted instead of the single one of the original model, a feature which permits binocular vision of the erect image of the parts under examination, and affords the stereoscopic effect which is so desirable in practice.

**Inspection Lamp.**

The only drawback of the slit-lamp is its comparatively high price. A type of lamp which can be held in the hand or fixed to a stand has recently been placed on the market under the name of inspection lamp by Messrs. Rayner & Keeler, Ltd., of Vere Street, Cavendish Square, London. This instrument can be used to a certain extent as a slit-lamp.

The lamp in its original form had been designed to give an intensely bright circular patch of light, free from unevenness due to the filament image, with the object of facilitating precise observation of the anterior parts of the globe. A circular plate with three apertures placed behind the condensing lens can be revolved to bring any aperture into the axis of the projecting or illuminating beam. In the newer models, one of the apertures is clear, the other is fitted with a coloured filter to meet individual requirements, while the third contains a lens system which enables the lamp filament to be projected as an extremely narrow band of light. In this latter condition, the lamp forms a useful and comparatively inexpensive slit-lamp.

By loosening the screw immediately behind the aperture plate the whole of the projection system can be removed, leaving only the lamp in position. A short tube with an opal disc and an iris diaphragm can then be placed in position so as to enable the observer to use the lamp for ophthalmoscopic or retinoscopic purposes.

**The Shape of the Cornea.**

To ascertain numerically the curvature of the corneal surface in its various parts, an ophthalmometer or keratometer is of course necessary. The description and the working

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of such instruments is beyond the scope of this work. A good idea of the shape of the external corneal surface and of its possible variations can, however, be obtained by means of the simple and inexpensive appliance termed the Placido disc, which consists of a disc about 25 cms. diameter on the surface of which concentric rings of equal depth and alternately black and white are painted. The centre of the disc is perforated by a sight hole which may, for the sake of convenience, be fitted with a magnifying glass.

The subject, sitting with his back to a well illuminated window, is directed to look at the centre of the disc by the observer at such a distance that he, the observer, looking at the subject's eye through the central hole or through the magnifying glass fitted in that hole, may see a clear image of the rings formed by reflection at the anterior corneal surface acting as a convex mirror.

It is clear that if the corneal catoptric images of the ring appear circular, then the portion of cornea which forms

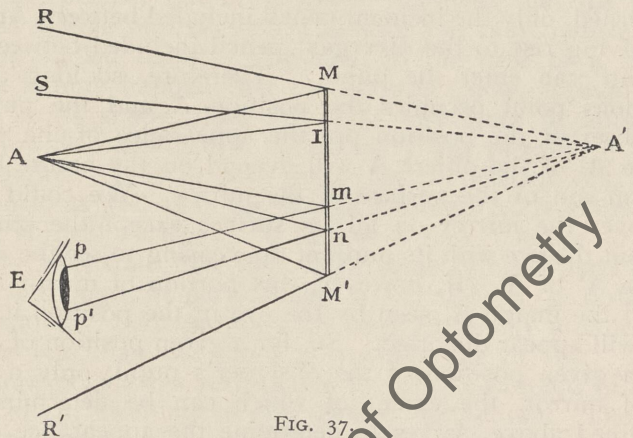


FIG. 37.

FIG. 37. To illustrate the fact that in the observation of the virtual image of a given object formed by a plane mirror and viewed by an eye occupying a definite position, only a small portion of the mirror intervenes, so that the appearance of the image depends on the regularity or lack of regularity of this portion of the reflecting surface.

these images is truly spherical. If on the other hand the corneal images of the rings appear elliptic or again appear more or less irregularly distorted, the portion of the cornea which forms these images is either regularly or irregularly astigmatic.

It should be well understood that the appearance of the images of the rings only conveys an idea of the curvature of the portion of corneal surface which forms these images.



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The matter will be made clear if we consider the working of a plane mirror. Let $MM^1$ (fig. 37) be a plane mirror and A a luminous point in front of it. We know that the effect of the mirror is merely to cause all the rays from A which strike it to be reflected as if they were really proceeding from a point $A^1$ symmetrical of A with respect to the mirror. Thus, a ray AI is reflected along IS as if proceeding from $A^1$. Likewise all other rays from A which strike the mirror are similarly reflected, so that the whole of the reflected rays are included between MR and $M^1R^1$, both of which are reflected as if they were proceeding from $A^1$, a point symmetrical of A with respect to the mirror.

Now let an observer's eye E be so placed on the path of the bundle of reflected rays that its pupil occupies the position $pp^1$. Amongst all the reflected rays, only those included between the lines $A^1p$ and $A^1p^1$ cutting the mirror at m and n respectively can enter the pupil; the reflected ray mp is due to the incident ray Am and the ray $np^1$ to the incident ray An. In other words and so far as the eye considered is concerned, only the incident pencil included between Am and An giving rise to the divergent pencil included between mp and $np^1$ can enter the pupil. Therefore, so long as the luminous point occupies the position A and the pupil of the observer the position $pp^1$ the appearance of the virtual image $A^1$ of the object A will depend on the nature of the portion mn of the surface of the mirror. We could paint or cover the mirror on all its surface except the part mn without the eye with its pupil at $pp^1$ ceasing to see the virtual image $A^1$ of A. If, however, this portion of mirror is distorted the image $A^1$ seen by the eye in the position it occupies will appear distorted. So, for a given position of object and a given position of the observer's pupil, only a small bit of mirror, the extent of which can be determined as explained above, serves to determine the appearance of the virtual image $A^1$ of the object A.

These considerations apply, word for word, to the case of a convex mirror and to the case of the cornea, acting as a convex mirror. Only in the latter case, since the observer looks at the corneal images through the centre of the disc, the regularity or lack of regularity of the corneal images of the rings will supply data as to the shape of the portion of cornea which is directed to the centre of the disc during the examination. It follows that if the subject looks at the centre of the disc, the appearance of the images will show whether the central portion of the cornea, i.e., the portion serving to vision in the ordinary way, is spherical or is regularly or irregularly astigmatic. Should the subject be

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then directed to turn his eye so as to fix a point on the horizontal diameter of the disc away from the centre, it will be seen that even if the corneal images of the circles were circular when the point of fixation occupied the centre of the disc, these images become more and more elongated in the horizontal direction when the point of fixation is shifted sideways; hence it is proved that even if the central portion of the cornea is regular and free from astigmatism the peripheral portion becomes less and less curved.

Beside the use of the Placido disc to ascertain at least roughly the presence or absence of corneal astigmatism in the central or visual zone of the cornea, this simple appliance is also useful to detect slight opacities of the cornea which might escape observation even by the focal illumination method. While well marked disease of the cornea is usually seen at a glance, yet we often observe cases in which there are patches of scarring due to previous ulceration. If well marked and whitish in appearance these constitute what is called a leucoma, but it frequently happens that the scars are less visible and of such a cloudy and faint nature that they are called nebulæ. Besides, in the case of a slight nebula it may happen that the corneal tissue, though distorted in its shape, does not show any trace of apparent opacity when examined in the ordinary way or even by focal illumination. It is in such cases that the Placido disc is of assistance, as well as in the case of a foreign body embedded in the corneal surface. It is not a rare instance to find subjects who state that they have some foreign particle in their eye though the particle may be invisible in the ordinary examination. Such particles are often extremely minute and perhaps less than the 100th of a millimetre in size. They are, however, always surrounded by minute droplets of tears and a slight swelling of the corneal epithelium. The eye being examined with the Placido disc, the corneal images are broken at the affected spot, which is thus easily recognised. Then again, we have those defects of the cornea known as "steamy" or "loss of polish." The reflected rings are then seen with serrated edges like the teeth of a fine saw and in any case the affected area shows a marked contrast to the clear definition of the remaining portions of the circles.

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## CHAPTER XIX.

### DISSECTION AND MICROSCOPIC SECTION MAKING.

The making of sections of the whole globe (similar to those which accompany this book, and are intended to be examined by means of a stereoscope) does not offer any serious difficulty.

A fresh eye easily procurable from any slaughter-house can be used as it is, but it is better to harden it, after all the muscles and fatty tissue from the outside of the globe are carefully removed.[1]

A good and easily obtainable hardening medium is formol or formalin, which consists of an aqueous solution of formaldehyde (40 per cent.). This solution, usually called commercial formalin and procurable from any chemist, is colourless and quite clear. To make the hardening fluid from it, it should be mixed in the proportion of one part of commercial formalin to 9 parts of distilled water or, still better, to the same amount of water to which 7.5 per cent. of salt has been previously added.

The fixing medium thus obtained is colourless, with a strong smell which irritates the mucous membrane of the nose and of the eye. The vapours causing this irritation are, however, not dangerous and the disagreeable sensations they cause soon disappear and do not leave any permanent injury.

The proportion of the mixing of the commercial formalin with water depends on the size of the organ or part of organ which is being investigated. To harden the whole eyeball, the above mixture, namely, one part of commercial formalin to nine parts of water, is satisfactory. The hardening takes about 24 hours. Moreover, any fresh eyeball can be preserved for a considerable time in a weaker solution (say 3 to 5 per cent.) and hardened in the solution stated just now when required for dissection. The different parts of the globe are not, however, regularly hardened and the sclerotic as well as the lens become considerably harder than the rest of the globe; hence the necessity of limiting the time of hardening in the above standard solution to about 24 hours at the utmost.

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[1] In the preparation of the portion of the present chapter which is concerned with Dissection, the author has obtained many useful hints from Dr. Woll's book on the Technique of Dissection of the Eye published in New York in 1924.

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The organs treated by formalin assume a special consistence, at the same time hard and somewhat elastic, like india-rubber. They can, therefore, be cut directly on being removed from the hardening fluid. A razor with one of its two surfaces quite flat is the best instrument to use for the purpose. A great advantage of formalin as a hardening medium is its rapid action. The main drawback is that besides abnormally hardening the sclerotic and the lens, it renders the latter opaque and, moreover, the choroid is so tightly compressed owing to the swelling of the vitreous which occurs while the specimen is in the solution that its true structure may be appreciably altered.

Another hardening medium often used is Müller's fluid, consisting of bichromate of potash 10 parts in weight, sulphate of soda 5 parts, distilled water 500 parts. The action is much slower and more regular than that of formalin and six weeks represents about the minimum time for the hardening of a globe.

Freezing a globe in an ordinary freezing mixture is a quick means of hardening, but all the tissues and parts of the eyeball do not freeze with the same uniformity, and besides, quite fresh tissues suffer appreciably in the freezing and the consecutive thawing.

Whichever method is used, the student will be able to make for himself sections of the globe in various directions and to obtain the views represented by the stereograms III. to XIV. which accompany this book.

The necessary material consists of a razor, one or two scalpels, a pair or two of forceps or tweezers, and a pair or two of scissors of different sizes. A few wide-mouthed vials are required to keep the various preparations in a preserving fluid for further examination, and some shallow glass trays, lined at the bottom with cork, are useful for the purpose of examination of the specimens under water.

A satisfactory dissection of the globe can only be made when the eyeball is freshly removed from the orbit. It follows that proper specimens of human eyes are not available in the ordinary dissecting room of a medical school. As pointed out in the preface to this book, the eyeballs which were used to prepare the stereograms we show were removed a very few hours after death, but as this is not practical for the optical student he should procure eyeballs of the pig, the sheep or the ox, which suit the purpose very well. It is essential, however, that the student should complete his study by the examination of a fresh human eye, and it is for this reason that we have reproduced the most interesting sections belonging to the set published by Dr. A. Thomson.

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In point of size and also in all particulars, the eyeball of the pig most closely resembles the human eyeball. It should be removed from the orbit before the animal is scalded in boiling water, which would alter some of the parts. On the whole, however, it is perhaps better that the student should begin with the bigger eyeball of an ox, since the dissection can be carried out more easily.

The first thing to do is to remove the conjunctiva, the capsule of Tenon, the extra-ocular muscles and the fatty tissue which adheres to a globe removed without precaution from its orbit. Pinching up with a pair of forceps the conjunctiva and the capsule of Tenon close to the corneal margin, the student should snip through these layers with a pair of scissors and divide them completely round the edge of the cornea. It is now easy to strip all the soft parts from the surface of the sclerotic coat, working steadily backwards towards the entrance of the optic nerve. A little behind the equator of the globe, the venæ vorticosæ (or vorticose veins) will be noticed issuing from the sclerotic coat at wide intervals from each other and, approaching the posterior aspect of the eyeball, the posterior ciliary arteries and the ciliary nerves will be seen piercing the same coat around the entrance of the optic nerve. To obtain a general conception of the parts which compose the globe, the best way is to select two specimens and to make sections through them in two different planes. One specimen may be divided by an equatorial plane into an anterior and a posterior half, whilst the other may be divided by an antero-posterior or sagittal plane into a medial and a lateral half. As already stated, these sections cannot easily be made with a knife on the globe as it is. A previous hardening is necessary by means of a formol solution or of Müller's fluid or, if this is impossible, freezing may be resorted to. In the latter case, the specimen should be placed in a tin box and surrounded by the ordinary freezing mixture of ice and salt; two or three hours are required to complete the process.

**Equatorial Section of the Globe. Study of the Posterior Half.**

For the study of the interior of the eye and its contents *in situ*, either a fresh eye or a hardened eye will do, though the latter is preferable for the sake of convenience. All the muscles and the fatty tissue outside the globe are removed from the surface of the globe, and the eyeball is then divided by an equatorial section into two halves, an anterior and a posterior one. The cutting of the sclerotic as well as that of the underlying parts (choroid, retina and vitreous) is better done by means of a pair of large scissors since a

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knife or a scalpel will tend to tear some of the most delicate parts. An ordinary safety razor blade is, however, an excellent instrument for cutting the globe into two halves because it cuts through the tissues without tearing them in any way.

When the globe is thus halved, a dark-coloured viscid fluid escapes; this fluid is really the perichoroidal lymph and not the aqueous humour as is sometimes stated. The posterior half or posterior hemisphere of the globe should be dealt with first, as it is easier to handle than the other half. In this half the retina is readily seen through the vitreous, and the choroid with its iridescent tapetum through both vitreous and retina. By simply tilting the half eye under examination and pushing the vitreous out with the finger, the latter medium is easily removed. It may happen, however (and this is especially so if one deals with an eye hardened in formalin), that the vitreous is closely adherent to the retina. In this case, the removal of the vitreous without injury to the retina is a matter of patience and care; the use of scissors and scalpel may become necessary, but even in these circumstances it is often sufficient to take hold of the half globe, to turn it so that the vitreous is downwards, and then to shake it gently until the vitreous separates itself from the retina and drops down.

After the vitreous has been removed, it should be carefully examined and its glassy appearance noted; it is owing to this appearance that the vitreous is sometimes called the hyaloid body. On attempting to pull it apart with the fingers, it will be found that it seems to hold together, this being due to the network of fibres which enters into its constitution.

Whichever way the vitreous has been removed from the posterior hemisphere of the globe the retina is usually left rather badly wrinkled and out of place. If the last method of vitreous removal has been used (and it is certainly the best) the retina is left in an entirely collapsed and folded state. To straighten it, the half globe should be placed in water, the inside surface uppermost; the retina will gradually unfold itself and lie flat against the subjacent choroid. When this is done, the eye should be carefully removed from the water with a pair of tweezers, tilted so as to empty it of all water, and placed downwards on a dry glass tray and allowed to drain itself.

Note the thinness of the retina and the apparent iridescence of the choroid showing through it. The optic disc and the physiologic cup are easily recognised, though obviously neither will appear as large as when the living eye is viewed with the ophthalmoscope.

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The retinal blood-vessels, as they ramify and branch after their entrance through the disc, are plainly seen, and a closer inspection shows in the centre of the disc a whitish pointed vessel usually 1 or 2 mms. long, which is the sloughed off and atrophied end of the hyaloid artery—the artery which, in the embryological state, ran forward from the central artery of the retina through the hyaloid canal (or Stilling's canal) to the posterior surface of the lens.

With the forceps, the peripheral edge of the retina can be picked up and, by pulling gently upwards, is torn away from its apparent place of attachment to the entrance of the optic nerve. When this has been done it will usually be seen that some threads protrude from the optic nerve; these strands, which are really optic nerve elements, can be separated by filling the half globe with water which is left in it for some time.

After the removal of the retina, the iridescence of the choroid due to the tapetum lucidum may be examined with a magnifying glass, or, a piece of choroid may be cut off and viewed under the microscope, as we shall see presently. Of course, this iridescence is not observed in the human eye, in which the tapetum is absent.

When the choroid is removed, and this is done in the same way as the retina itself is separated from the choroid, the inner surface of the sclerotic is laid bare. Its brownish colour, more or less marked, is due to a variable amount of pigment in the cells of the inner layers (suprachoroidal membrane) and also to a slight extent to the staining influence of the perichoroidal fluid.

The posterior hemisphere of the globe which has served to the previous demonstration can also be used to study the arrangement of the head of the optic nerve. In cutting the nerve away from the sclerotic it is well to leave at least 5 mms. of sclerotic attached to it. It will facilitate the handling. With the thumb and forefinger of the left hand the nerve is held on the table so that it is straightened out lengthwise, and then with a scalpel, or better still with a safety razor blade, the nerve is cut in two longitudinally. The cutting should be done with one movement otherwise the nerve will be hacked and will not make a good specimen. This specimen will show the way the fibres are arranged. A cross section of the nerve can be cut from another eye and the two sections should be compared.

The cross section of the nerve will show the sheaths of the nerve better than the longitudinal section. If it happens by good luck that the longitudinal section is cut through

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the central blood-vessels of the retina, these vessels appear as rather thin dark streaks.

**Study of the Anterior Half of the Globe.**

The anterior half of the globe will show the lens *in situ*, the ciliary processes, the posterior aspect of the iris and of the lens, and the ora serrata, but if the globe has been cut too far forwards of its equator the ora serrata will not be present.

The ciliary processes and the posterior lens surface are seen to better advantage when the vitreous is removed from the anterior hemisphere. This removal is carried out with dull-pointed tweezers by catching hold of the vitreous at any part of its free or cut margin and stripping it off both the ciliary processes and the lens, using a prying, pulling, movement to do so. The layer of pigment cells forming the pars ciliaris retinæ which covers the inner surface of the processes may be removed by picking it carefully with the tweezers. The processes will then be seen of a whitish colour. The pupillary edge of the iris rests upon the capsule of the lens, but the nearer the approach to the periphery, the farther the iris is from the lens; thus are formed the anterior and posterior chambers of the eye. To gain a clearer conception of the construction of these chambers, a sagittal section of the globe is better than an examination of the anterior hemisphere specimen.

The lens can now be removed, using a fine knife to cut through the suspensory ligament close to the lens margin. When this is done there will be seen in the anterior chamber the thin watery fluid we have described under the heading of aqueous fluid.

The corona ciliaris and the orbiculus ciliaris may be best seen if viewed with a magnifying glass.

To see and study the iris, the cut edge of the choroid is taken with the tweezers and, by gentle pulling, is separated from its attachment to the sclero-corneal junction. The white ring on the anterior surface of this part of the uveal tract is the ciliary ring. With scissors, this ring is cut round at its outer edge. The specimen will then show the anterior surface of the iris, and on its posterior side it will exhibit the close relationship between the iris and the ciliary processes.

After the anterior hemisphere has had everything removed from it, it is reduced to the first or outer tunic of the eye, namely, the anterior portion of the sclerotic and the cornea. The cornea does not exactly fit in the sclerotic as a watch glass in its rim; holding the specimen to a strong

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light, it will easily be seen that the sclerotic seems to overlap the cornea, especially in the vertical meridian.

By using the tweezers, the cornea may be split, but nothing in the way of locating its layers can be recognised unless a section is made for microscopical examination (see page 394). The superficial part of the cornea may be scraped off, especially if the specimen is somewhat dry; the portion thus removable is the corneal epithelium reduced to a thin layer of flattened cells.

**The Crystalline Lens.**

To study the crystalline lens properly it is advisable to deal both with an eye which has not been hardened and with an eye or a lens that has been kept for about two weeks in a 5 per cent. solution of formalin. In the fresh state the lens is too friable to permit of much handling. The following dissection should be made, however, to ascertain the clearness of the lens substance, its magnifying power, its attachments, its capsule, etc.

To remove the lens it is necessary to separate the suspensory ligament, using for the purpose a pair of small pointed scissors. The capsule may be removed by picking it up on the periphery of the lens and stripping it off; it will peel off in the same way as the outer skin of a pea does.

The three radiate lines on both surfaces of the lens will not be as clearly seen on a fresh eye as on the lens of an eye which has been previously hardened, but a close inspection with a magnifying glass will no doubt render them apparent.

An attempt should be made to separate with the point of a scalpel the outer layer of the lens (the cortex) from the central or inner part, the nucleus. This may not be very successful in a fresh eye, though the operation is suggested for the purpose of comparison when the same thing is done with a hardened lens.

It will be found that the lens which has been kept in formalin is no longer transparent, but only more or less translucent. When viewed by transparency, the three radiate lines on each surface will be seen to begin at the pole and to radiate towards the equator. These lines usually form on each surface an angle of 120° with each other so that they represent a capital Y on the posterior surface and an inverted capital Y on the anterior one, each of these radial lines thus forming an angle of about 60° with the neighbouring ones on the other surface.

To study the laminated structure of the lens, it is best to boil the lens by dropping it into boiling water, where it

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should be left for two or three minutes. A longer period would cause a distortion of the structure under investigation and make it so fragile that it could hardly be handled without falling to pieces. The point of a scalpel is then inserted carefully at one pole and lifted gently in the direction of one of the radiating lines; this will tend to raise one of the concentric layers which can easily be peeled off. The operation is repeated in the direction of the other radiating lines. Examining with a magnifying glass the exposed surfaces and the layers as they are peeled off will show plainly the arrangement of the lens fibres and their direction. Another view of the onion-like layers of the lens is obtained by cutting through with a safety razor blade, either longitudinally or equatorially. It is best to make both sections on separate lenses. The layers are more readily seen if the lens has been previously stained with chromic acid or more simply if it is dropped, immediately before cutting, into a solution of carmine; red ink slightly diluted is a good substitute for carmine.

A lens that has been boiled and partly dissected may be kept indefinitely in a 5 per cent. solution of formalin. The fibres, the concentric layers and the laminæ in such a specimen are always interesting.

It is possible to restore a fair degree of transparency to a lens which has become translucent by boiling or by immersion in a hardening fluid. It should be placed in alcohol at 50 per cent. for several hours, then drained on blotting paper and placed in alcohol at 75 per cent. The lens is then transferred in alcohol at 85 per cent. for 10 or 12 hours, after which it is immersed in absolute alcohol, where it is left for another period of 10 or 12 hours, or even longer. This process, which is termed "running through the alcohols," is followed by a careful drainage on blotting paper, care being taken to change the paper or to move the lens on it till all moisture is removed. The effect of these operations is to dehydrate the lens as completely as possible. If the capsule has not been previously removed, a small amount of alcohol may remain between the lens and the inner surface of the capsule; this must be removed either by puncturing the capsule with a needle or by removing the capsule entirely. To complete the operation the lens is placed in xylol or in benzine. After about 24 or 36 hours, the softer cortex will be quite clear, but the nucleus will be still cloudy. At the end of a week, the whole lens should be quite clear and transparent.

The time required for a complete clearing depends very much on the size of the lens, and the period stated just now

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applies to a small lens (pig, calf or sheep). The larger lens of the ox may take two weeks to recover its transparency, and the necessary period is longer when the lens has been boiled than when it has simply been hardened.

Cedar oil may be used for the purpose of clearing after the process of running through the alcohols, but it renders the lens slightly yellowish and does not restore the same transparency as xylol or benzine.

The longer a lens is left in the clearing medium, the harder and the smaller it becomes. At the end of six weeks or two months, it is so hard that it can no longer be cut with a knife, and if it is desired to halve it, a fret-saw is necessary.

**The Eye Kernel.**

Beside studying separately the coats and media of the eye as we have done just now, it is interesting to proceed to an examination of what is often called the kernel of the eye, i.e., the vitreous body together with its hyaloid membrane, the lens and the zonule of Zinn.

This examination may be facilitated by placing the eye in a strong solution of picro-carmine for a few minutes; when removed from the staining fluid and well washed in water, the hyaloid membrane of the vitreous, the capsule of the lens and the zonule of Zinn are deeply coloured in red and their connections become very apparent.

Whether this staining is carried out or not, the dissection is easier to perform on an eye (sheep or pig, or preferably ox) which has not been hardened but has been merely kept for two or three days in a cool place in order to allow it to collapse a little. It is a fact of observation that if an eye is quite fresh, the ciliary processes are not easily separated from the hyaloid membrane, and the same thing occurs if a preserving or hardening medium has been used.

With a pair of fine dissecting forceps, the sclerotic is picked up 5 mms. in front of the equatorial plane and an incision is made in it with fine pointed scissors. Then, the globe being held in the left hand without exerting a pressure on it, the point of the scissors is inserted in the incision and the sclerotic cut, care being taken to keep the point of the scissors close to the sclerotic in order to avoid an untimely puncture of the choroid. The cutting of the sclerotic is continued on a line parallel to the equatorial plane till about half of it is separated.

In this cutting the point of the scissors should be moved forward with a slight oscillatory and lateral movement, and while this is done, the globe should be partly suspended

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from the point of the scissors in order to loosen the choroid from the sclerotic and to prevent a possible puncture of the former membrane at this stage. Then, pressure is exerted in such a way that the lips of the cut portion of the sclerotic gape a little. In this gap the scissors are inserted and their point is used to pick up the choroid and the retina which are then cut in their turn. Should the choroid alone be separated the retina will show a milky white or yellowish white underneath; in such a case, the retina must also be cut, care being taken not to cut too deeply or the hyaloid membrane might be damaged. The cutting of the retina and choroid is continued for a length of about 20 mms., pressure being occasionally exerted upon the globe in order that the vitreous may be forced upwards above the cut choroid and retina. This will show whether any strands of the two membranes are left. If the separation is complete on the distance specified above, the eyeball is inverted, squeezed and gently shaken over a glass disc containing a weak (3 to 5 per cent.) solution of formalin, when the hyaloid membrane containing the vitreous, the zonule of Zinn and the lens will drop out intact as when one empties the contents of an egg.

It often happens that a certain amount of pigment remains attached to the zonule; this is easily removed by scraping it with the edge of a scalpel or by brushing it off with a wet brush. It is not advisable to use alcohol as a preserving medium if the above preparation is to be kept for further study. Alcohol would produce an almost immediate opacity and hardness which would spoil the specimen. The best way is to place the kernel in a bottle containing a 5 per cent. solution of formalin. It can then be kept for a considerable period and can be examined at leisure with the help of a magnifying glass if necessary.

The so-called canal of Petit, i.e., the triangular space around the circumference of the lens and between the front and the back portions of the suspensory ligament, can easily be demonstrated by blowing air into it. A blow-pipe is generally too large for the purpose, but the tapering end of a glass medicine dropper is useful. The inflation of the canal of Petit is easily carried out on the specimen which has been obtained in the previous dissection, after it has been kept for about ten days in the formalin solution, when it becomes hard and tough enough to stand a considerable amount of rough handling. The preparation is removed from the solution and placed on a glass tray, the lens being uppermost. The tapering end of the glass dropper or the end of the blow-pipe is then introduced through the fibres of the suspensory ligament close to the lens margin. A

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gentle blowing through the tube will soon show the sacculated appearance of the canal of Petit. It may be necessary to move the pipe in or out in order to find the canal, and all the while, blowing is carried out steadily.

**General Conclusions Derived from the above Dissections.**

The dissections we have described will enable the student to get a good idea of what may be learnt of the general anatomy of the eye, by mere observation with a naked eye or, if necessary, with a magnifying glass.

**The Outer Ocular Coat or Sclero-Corneal Coat.**

It will be seen that the outer tunic of the eye or the sclerotic, which is commonly called the white of the eye, appears as a dense resisting fibrous membrane, opaque white or more exactly translucent, and forms the posterior five-sixths of the globe. It is thickest behind and becomes thinner as it is traced forwards. Near the corneal junction, however, it again becomes thicker owing to the fibres it receives from the tendons of the extra-ocular muscles. Except at the optic nerve entrance and a little behind the sclero-corneal margin, where it adheres to the subjacent structure, the deep surface of the sclerotic is very loosely attached to the choroid. Some pigmented strands or trabeculæ of connective tissue pass between the two coats and form what is really an extensive lymphatic space.

The point at which the optic nerve pierces the back part of the sclerotic does not correspond to the posterior pole of the globe but is situated about 3 to 4 mms. to the inner (nasal) side of the posterior pole and very slightly above it.

Here, the outer fibrous sheath of the optic nerve, which is derived from the dura mater of the brain, blends with the sclerotic coat, whilst the bundles of optic nerve fibres are carried forwards through a series of small openings in the inner portion of the sclerotic and in the choroid, this perforated or sieve-like portion being the lamina cribrosa.

The sclerotic is also pierced by numerous blood-vessels and nerves. Thus, the long and short posterior ciliary arteries, together with the ciliary nerves, perforate the sclerotic round the optic nerve entrance. Four or sometimes five venæ vorticosæ issue from the interior of the globe by piercing the sclerotic a little way behind the equator at wide intervals from each other. The anterior ciliary arteries pierce the sclerotic near the corneal margin.

In front, the sclerotic is not only contiguous to but is directly and structurally continuous with the cornea. The

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region where the sclerotic passes into the cornea (sclero-corneal junction) is marked by a faint groove which receives the name of scleral sulcus (see stereogram III.). At the junction, the sclerotical tissue slightly overlaps the corneal tissue so that the line of union, when seen in section, is oblique. Close to this, a minute canal in the substance of the sclerotic, termed the canal of Schlemm, encircles the margin of the cornea.

The cornea itself forms, as we have seen, the anterior sixth of the outside coat. It is transparent in the fresh state and its curvature is more accentuated than that of the sclerotic; thus it constitutes a segment of a smaller sphere. Viewed from behind it appears circular, but looked at from the front, it is seen to be slightly wider in the transversal direction; this is due to the fact that the sclerotic overlaps the cornea to a greater extent above and below than sideways. The posterior (concave) corneal surface forms the front boundary of the anterior chamber and is separated by the aqueous fluid from the front surface of the iris.

The anterior surface of the cornea is covered by the bulbar conjunctiva, which is here reduced to its epithelial layer. On the posterior surface we find the elastic glassy structure we have described as the elastic membrane of Descemet, but such details of structure can only be recognised in a microscopic examination. When the cornea is relaxed, Descemet's membrane becomes wrinkled and can be torn away in shreds from the proper corneal tissue; when dealt with in this way the portions removed show the tendency to curl up, which is characteristic of elastic membranes.

At the margin of the cornea, Descemet's membrane becomes fibrillar and some of its fibres are continued into the iris to form the pillars of the iris or the ligamentum pectinatum while others are prolonged backwards into the choroid and the sclerotic. The ligamentum pectinatum bridges across the angle formed by the cornea and the iris, and the bundles of fibres into which Descemet's membrane breaks up in this region constitute an annular meshwork or a sponge-like series of minute spaces termed the spaces of Fontana or the filtration angle (page 200). The details of structure of the filtration angle can only be made out by a microscopic examination.

When the above dissection is successfully carried out, the outer or sclero-corneal coat is isolated in two portions, whilst a continuous view is obtained of the intermediate vascular coat (uveal tract). The eyeball thus denuded of its external coat can be placed in a shallow vessel filled with

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water, when the appearance of the external surface of the uvea (which has been described in page 174) is very easily seen.

**The Uveal Coat.**

The uveal coat can be seen in its entire extent when the dissection of the external coat has been carried out as explained above.

It should be remembered that the uveal tract consists of three parts: the choroid coat proper, the ciliary body, and the iris.

The choroid coat is pierced behind by the optic nerve and is somewhat thicker behind than in front. The outer or superficial surface is connected with the sclero-corneal coat by the lax tissue (suprachoroidal membrane) we have already alluded to. Its deep surface is moulded over the retina and connected with a single layer of deeply pigmented cells (hexagonal pigment epithelium of the retina) which usually adheres to the choroid when the latter is separated from the subjacent structure, though in reality it must be regarded as a portion of the retina (see page 215).

The minute structure of the choroid can only be ascertained under the microscope, when it appears to be made of a closely meshed layer of capillary vessels on the side corresponding to the retina and of two other vascular layers, the layer of medium-sized vessels and the layer of large-sized vessels. The veins of the choroid ultimately group to form the venæ vorticosæ. Pigment cells are found in the interspaces between the vessels of the last two layers, and are more abundant in the layer of large vessels than in the layer of medium-sized vessels. Normally there are no pigment cells in the choriocapillaris layer.

We have shown before how the arrangement of the anterior hemisphere of the eye can be studied from a dissection and an examination of the half globe cut as explained in page 358. Another way of proceeding to this study consists in dissecting away the outer or sclero-corneal coat of an eye and placing the specimen thus obtained in a dish containing water. If the pigment coating the outer surface of the choroid is carefully washed out with a wet camel-hair brush the superficial veins of the choroid will then appear in white curved lines converging towards four or five points from which the venæ vorticosæ take their origin.

The arrangement and structure of the ciliary muscle can only be investigated by microscopical examination, when the fibres constituting it can be seen to be made of two main sets, viz., a radiating set and a circular one.

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The radiating fibres arise from the deep aspect of the sclerotic coat, near the margin of the cornea. From this point, they radiate backwards in a meridional direction and gain insertion in the choroid coat; they constitute the part of the ciliary muscle termed the tensor of the choroid or muscle of Brucke.

The circular fibres consist of two or three bundles placed upon the deep aspect of the radiating fibres and form a muscular ring or a sphincter around the circumference of the iris. This portion of the ciliary muscle is called Müller's muscle. There is no sharp line of demarcation between the meridional and the circular fibres of the ciliary muscle, some fibres forming a zone of transition between the two main sets.

To obtain a view of the ciliary processes, a coronal transversal section of the globe should be made in a direction parallel to and a short distance in front of the equatorial plane of the eyeball. The vitreous body occupying the anterior segment of the globe should be carefully removed. When this is done, the deep aspect of the ciliary processes will be seen as they radiate backwards from the circumference of the lens. By washing out the pigment from this part of the uveal tract, the arrangement of the processes will be more plainly displayed.

To expose the ciliary processes from the front, another eyeball is required. The cornea is removed with a pair of scissors by cutting round the sclero-corneal junction. The iris is thus brought into view and may conveniently be examined *in situ* at this stage. Several cuts in the meridional direction should then be made in the anterior part of the sclerotic at equal intervals. The strips of sclerotic should be separated from the ciliary muscle and pinned backwards in a cork-lined tray filled with water. The last step in the dissection consists in the removal of the iris.

In this way it can be seen that as the choroid is traced forwards under the ciliary muscle it forms a series of elongated prominent thickenings which radiate backwards from the margin of the lens like the folds of a goffered frill. These thickenings vary slightly in their degree of prominence and also in length, but they are very constant in number. In the human eye 70 ciliary processes may as a rule be counted. As each process proceeds forwards, it becomes gradually more and more prominent until ultimately it ends in a thickened projection which occupies the space between the margin of the iris and the circumferential part of the anterior lens surface. In this position the processes bound peripherally the posterior chamber of the eye.



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The ciliary processes rest upon the subjacent zonule of Zinn. This is adapted in the most intimate manner to the ciliary processes. It is folded or wrinkled in such a way that the folds occupy the valleys or sulci between the processes.

The iris has been fully described in page 187. It is separated from the cornea by the anterior chamber filled with aqueous humour and is continuous by its circumference with the choroid coat, while at the same time it is connected by the pectinate ligament with the sclero-corneal margin. The iris is circular in form and is perforated at its centre by an opening termed the pupil. Its anterior surface is finely striated and shows a different coloration in different subjects. The back surface is deeply pigmented and is furthermore lined by a pigmented layer derived from the retina (pars iridica retinæ) which extends up to the pupillary margin.

It has been pointed out that during life the pupil constantly varies in its dimensions so as to control automatically the amount of light admitted in the eye. These changes in the size of the pupil are produced by the contractile properties of two groups of involuntary muscular fibres. One group is made of fibres arranged circularly around the pupil in the form of a sphincter; the second group consists of fibres which have a radial direction and pass from the pupil to the circumference of the iris so as to constitute a dilator muscle, of a special character, as has been explained in page 188.

Though the human pupil is practically circular, it should be observed that in the sheep and the ox it is greatly elongated in the transversal direction. In the pig, however, it is approximately circular.

The ciliary nerves, which arise from the ciliary ganglion and from the nasal nerve, after piercing the sclerotic at the back of the globe around the optic nerve, extend forwards between the sclerotic and the choroid. They will be seen on a specimen in which the sclerotic has been partially cut and turned backwards in separate flaps, under the form of fine white filaments. In the posterior hemisphere, they occupy grooves on the inner surface of the sclerotic, and can only be separated from it with difficulty. Reaching the ciliary zone, the nerves break into branches which join in a plexiform manner and send twigs to the ciliary muscle, the iris and the cornea.

The arrangement of the blood-vessels of the globe has been fully described (page 335). It should be remembered that, apart from the retinal circulation, there are three groups

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of ciliary arteries which supply the whole globe except the retina or more exactly except the innermost layers of the retina.

The short posterior ciliary arteries, branches of the ophthalmic artery, pierce the sclerotic around the optic nerve entrance and are distributed mainly to the choroid. The long posterior arteries, also branches of the ophthalmic artery, are only two in number and perforate the sclerotic on either side of the optic nerve, a short distance from the short ciliary arteries. They are carried forwards between the sclerotic and the choroid; when they reach the ciliary zone, each artery divides into an ascending and a descending branch, and these, together with the short ciliary arteries (see below) form an arterial circle termed the major circle of the iris (circulus iridis major).

From this circle, branches are given to the ciliary muscle, ciliary processes and to the iris. The minor circle of the iris (circulus iridis minor) is the name applied to a second arterial ring in the iris at the outer border of the sphincter. The anterior ciliary arteries are very small twigs which enter the sclerotic close to the margin of the cornea and take part in the formation of the major circle of the iris and at the same time send fine branches to the ciliary processes.

All the venous blood of the choroid is collected in the venæ vorticosæ which ultimately empty their contents into the ophthalmic vein.

**The Retina.**

To view the retina in the hinder part of the eyeball which has been cut into two parts to expose the ciliary processes from behind, the choroid is raised from the inner surface of the sclerotic under a flow of water from a tap; then the venæ vorticosæ entering the deep surface of the sclerotic are brought into view. When these are divided, and the separation of the two coats (choroid and sclerotic) is carried back to the optic nerve entrance, the short posterior ciliary arteries as they emerge from the sclerotic and enter the back part of the choroid will be seen.

In the portion of the globe from which the sclerotic and cornea have been removed, the iris, ciliary processes and the choroid should be carefully stripped off piecemeal under water; this will expose the retina.

The retina may be regarded as made of two main strata, namely, a thin pigmentary layer which adheres to the deep surface of the choroid and is usually removed with it, and a delicate nervous layer, the retina proper, which is

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moulded over the surface of the vitreous but presents no attachment to it except at the entrance of the optic nerve. The latter layer extends forward beyond the equator of the globe and, a short distance in front of the ciliary zone, it appears to end in a well defined wavy or indented border termed the ora serrata. This appearance, however, is deceptive; the nervous elements truly come to an end at this border, but a lamina, which is formed of the framework of the retina deprived of the nervous elements, is prolonged forward as far as the pupillary margin. The portion of this lamina in relation with the ciliary body is extremely thin and cannot be detected with the naked eye; it is termed the pars ciliaris retinæ. The portion extending over the back surface of the iris is thicker, more pigmented and constitutes the iridic part of the retina (pars iridica retinæ).

During life the retina proper is transparent, but after death it soon assumes a dull greyish tint and becomes opaque. Posteriorly the retina is tied down at the optic nerve entrance and when viewed from the front this spot appears as a conspicuous circular disc, the porus opticus or optic disc. The optic disc, in correspondence with the entrance of the optic nerve, lies to the inner (nasal) side of the antero-posterior axis of the eye. Exactly at the point where the visual axis cuts the posterior wall of the eye, there is in the human eye a small yellowish spot termed the macula lutea (or yellow spot). It is somewhat oval in outline and depressed at its centre, thereby forming what is termed the fovea centralis. It is to be noted that there is no macula in the eyeball of animals, except perhaps in the higher species of monkeys.

In a fresh eyeball the central artery of the retina will be seen entering the retina at the optic disc; as we have already seen, it immediately divides into an ascending and a descending branch and each of these breaks up into a large outer (temporal) and a smaller (nasal) division. These ramify in the retina as far as the ora serrata, but the different branches do not anastomose with one another nor with any other vessel in the eyeball. The retinal veins converge upon the optic disc and disappear into the substance of the optic nerve in the form of two main trunks which soon unite with one another.

The retinal vessels, the optic disc and the macula can all be examined in the living eye by means of the opthalmoscope. The red reflex seen in the pupil of an eye illuminated by an ophthalmoscopic mirror when the observer watches the eye through the sight hole is produced by the blood in the choroid, the colour being more or less modified owing

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to the retinal and choroidal pigment, as well as by a certain amount of light reflected by the white sclerotic.

**The Refracting Media.**

The examination of the lens with its suspensory ligament and of the vitreous body enclosed in the hyaloid membrane is easy on the preparation of the eye kernel previously described.

The vitreous is a soft, yielding, transparent, jelly-like body which occupies the posterior four-fifths of the ocular cavity. The retina is spread over it but is only attached to it at the optic disc. Anteriorly, the vitreous is hollowed out for the reception of the posterior convex surface of the lens; this depression is called the fossa patellaris.

The substance of the vitreous is enclosed in a delicate transparent membrane, the hyaloid membrane. Extending forwards through the vitreous from the optic disc to the posterior pole of the lens, is a minute canal lined by a tube-like prolongation of the hyaloid membrane and containing a watery fluid. This is termed the hyaloid canal or the canal of Stilling and represents the path which was taken by a branch of the retinal artery, which in the fœtus extends forwards for the supply of the lens capsule but disappears before birth.

As a rule, the canal of Stilling is not visible in an ordinary dissection, but if the eye kernel be shaken up in the picro-carmine solution it is often rendered evident through the staining fluid entering it.

In the ciliary region, the hyaloid membrane of the vitreous becomes thickened and strengthened and forms what is termed the suspensory ligament or zonule of Zinn. As this approaches the equator of the lens, it splits into two layers, viz., an exceedingly delicate deep lamina which lines the fossa patellaris and a more superficial and stronger part which becomes attached to the front of the lens capsule.

The zonule lies subjacent to the ciliary processes and is radially plaited or wrinkled in correspondence with these; thus the elevations or wrinkles of the zonule extend into the intervals between the ciliary processes while the ciliary processes in their turn lie in the depressions between the wrinkles of the zonule. When the eye is fresh, these opposing parts are closely adherent.

The zonule of Zinn is strengthened by radially directed elastic fibres, and after the delicate lamina which lines the fossa patellaris is given off from its deep surface, it extends forwards as a distinct layer and is attached to the anterior surface of the front capsule of the lens a short distance

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beyond the margin of the latter structure. In this manner the suspensory ligament of the lens is formed, but this is not the only attachment of the suspensory ligament. Some scattered fibres are attached to the circumference or equator of the lens (equatorial fibres), while some others are fixed to its posterior surface, near to its margin (post-equatorial fibres). In this way, the lens is held firmly in its place in the fossa patellaris. The canal of Petit, i.e., the lymph space which surrounds the equator of the lens and is bounded in front by the suspensory ligament and behind by the hyaloid membrane, has been mentioned before when it was pointed out that by introducing a fine blow-pipe into it through the suspensory ligament, it can be partially or perhaps completely inflated with air, when it presents a characteristic sacculated appearance.

The crystalline lens may be removed by snipping the suspensory ligament with scissors. The lens *in situ* appears as a biconvex transparent structure lying in front of the vitreous body and behind the iris. It is enclosed within a glassy elastic capsule to which the different parts of the suspensory ligament are firmly attached. It represents for study an anterior surface, a posterior surface and a circumference or equator. The anterior surface in a living eye at rest is not so curved as the posterior surface. The central part of the anterior surface corresponds to the iris and looks forwards in the anterior chamber. Around this part, the margin of the pupil is in contact with the lens, whilst nearer to the equator the lens and the iris are separated by the aqueous fluid filling the posterior chamber. The back surface of the lens, more curved than the anterior one, rests in the fossa patellaris of the vitreous body. The equator of the lens is circular and forms one of the boundaries of the canal of Petit.

Faint radiating lines can be seen on both surfaces of the lens and give a clue to its structure; they indicate the planes along which the extremities of the lens fibres come into apposition with each other. The capsule is an elastic, glassy membrane, considerably thicker in front than behind; the thickness of the capsule varies appreciably in different zones of a same specimen.

If in an eyeball the cornea and the iris of which have been removed, the anterior wall of the lens capsule is divided with a sharp knife, a slight pressure will cause the lens itself to escape through the opening.

If the lens body be compressed between the finger and the thumb, it will be observed that the outer portion or cortical

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part is softer whilst the central part or nucleus is much firmer. Should the lens be hardened or boiled, it can easily be ascertained that it is made of numerous concentrically arranged laminæ, as has been described previously.

**Dissection of the Appendages of the Eye.**

The dissection and study of the appendages of the eye (lachrymal apparatus, conjunctiva, lids) and of the extra-ocular muscles is not such a simple work as the previous dissections. However, the student will be well advised to attempt it.

The best way is to procure the head of some animal, preferably a calf's head because of its size. The lower jaw may be removed by the butcher supplying the head in order to have a less bulky piece of material to handle.

Close to the inner canthus, i.e., on the inner side of the free margin of each lid, a little rounded eminence is found which is termed the lachrymal papilla; in the centre of this papilla a small opening, the lachrymal point, can be seen. The lachrymal point of the lower lid is easier to see than that of the upper one. The reason for this is that normally the puncta are in apposition to the globe and constantly immersed in the small collection of tears we have described as the lachrymal lake. Therefore, to see the puncta, the lower lid has to be drawn down while the upper one has to be everted.

A blunt and fine knitting needle slightly lubricated with vaseline is inserted in the lower punctum and pushed first inwards, towards the inner canthus; it penetrates in the lower canaliculus which runs in the thickness of the lid margin and opens into the lachrymal sac, which itself is in communication with the nasal duct. When the end of the needle meets the bone forming the inner wall of the orbit it is turned in a vertical direction, so as to pass into the lachrymal sac and into the nasal duct.

A similar operation can be performed with another needle on the upper punctum, though this is a little more difficult. If each needle is left in its position when the end reaches the bony orbital wall it will be found that they meet each other in the lachrymal sac, a fact which is not surprising considering that, as we have pointed out, the two canaliculi open in the sac. From the puncta to the place of meeting of the two needles the course of the canaliculi is shown up to their junction as they both open into the lachrymal sac. With small scissors the canaliculi may be loosened from the surrounding lid tissue, or, a scalpel may be used to lay open the canaliculi, cutting along the top of the needles.

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The cilia, the lids, the palpebral and the bulbar conjunctiva may be examined without dissection.

An examination of the lids will show the openings of the ducts of the Meibomian glands a short distance posterior to the insertion of the cilia. Very fine greased needles may be easily inserted for a short distance into some of the ducts and a dissection is made along the course of the ducts thus outlined by the needles. Or again, to see the glands themselves there is only to slice through the ducts with a scalpel or a safety razor blade through the entire width of either lid. This will cut the glands into two parts and show their length, breadth and general arrangement.

The eyeballs obtained from a butcher or from a slaughter-house always have the extrinsic tissues so badly cut and torn that identification of the various parts and their relation is practically impossible. For this reason, and to study the orbital contents, it is better to procure the head of an animal, sheep or calf, and dissect the eye with all the extrinsic parts intact. For this purpose, a chisel and a hammer are necessary, in addition to the usual dissecting instruments.

Working, say, on the left eye, the first step in the dissection consists in making an incision directly over the supra-orbital ridge and extending from the inner to the outer canthus. At the middle point of that line, another incision is cut at right angles to it upwards to the top of the head. Next, a similar cut is made below the eye from one canthus to the other. The skin is loosened from the bone with a scalpel and the skull is laid bare immediately over the orbit. The flaps of skin are folded back and fastened down with pins or tacks so that they will not interfere wtih the rest of the work.

Using the hammer and chisel, the roof of the orbit is then cut through at the middle of the supra-orbital ridge and the section is continued upwards for 2.5 inches. It is necessary to avoid hard blows with the hammer, or the chisel might be forced through the underlying tissues. A peculiar sound is heard when the bone has been completely penetrated. The cutting is continued until the orbital roof is sectioned on a length of 2.5 inches. This being done the bone is cut through downwards to the right, beginning at the upper end, on a length of about 2 inches towards the outer canthus, and a similar line is cut on the other side of the centre towards the inner canthus. This will mark out two irregular triangular shaped pieces of bone; the right-hand piece is removed by prying it off and the left-hand piece should be pried loose and then carefully cut away with

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a scalpel so that the pulley of the superior oblique muscle may not be injured. In dealing with the orbital contents it is imperative to dissect close to the bone so that the periosteum be removed in the form of a sac or capsule in which the globe with all its extrinsic tissues is contained.

Should any difficulty be experienced in getting at the posterior part of the orbit, it may be necessary to cut away as much more of the obstructing bones as is required. In this way a sac or capsule containing the eye with its six external muscles, the lachrymal gland, and the lids, all *in situ,* will be removed. As the orbital entrance of the optic nerve is approached, care should be taken not to cut into the sac or sever any of the muscles.

The lachrymal gland is easily distinguished on the preparation by its pinkish appearance. It will be found to be made of two separate parts, an inferior and a superior one. In the living subject, the gland lies directly over the eye and near the outer angle of the orbit. In the enucleated eye it will be found to be near the outer canthus and over the globe. The gland may be dissected out of its position and examined more closely. A magnifying glass will show its racemose structure, which is even more apparent if the gland is cut into two parts.

To find the ducts of the gland, the outer and inner canthi of the enucleated eye should be cut across while the globe is pushed forwards and the lids backwards. This will expose the conjunctiva and the fornices. On the upper surface of the palpebral conjunctiva and near the outer canthus, a number of minute openings, generally eight to ten, will be seen on close inspection; these are the openings of the ducts. Needles or pins lubricated with vaseline may be inserted and pushed in these openings for a considerable distance and show clearly the course of the ducts.

To dissect the capsule of Tenon, all the superficial fat and connective tissue should be carefully removed from the enucleated eye. Though the capsule is usually described as a definite sac-like membrane of relatively considerable thickness with all its parts well defined, yet an attempt at dissection will show that it is not so easily discerned. The capsule will be found to be the thin, semi-transparent, fibrous membrane which surrounds every muscle as well as the posterior two-thirds of the globe and is continuous anteriorly with the ocular conjunctiva. An easy demonstration of its location and its various parts is afforded if a portion is pinched up and inflated through a fine blow-pipe.

After the lachrymal gland has been dissected away it is easy enough to remove the fat and the connective tissue

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surrounding the eye so as to investigate the extra-ocular muscles. The first thing to do is to locate the superior oblique. Having ascertained which is the inner side of the eye, the pulley is recognised as a little hard eminence. Then it is necessary to dissect around the pulley but not through it and to follow the muscle along to its origin. When the superior oblique is entirely freed, the action of this muscle can be readily demonstrated by holding the pulley, i.e., the tendinous ring, with the fingers of one hand while the muscle is pulled backwards or forwards with the other hand.

With the dissection of the capsule of Tenon and the superior oblique the work of isolating the other extra-ocular muscles is partly done. No special directions are required except that the pulley of the superior oblique should not be injured or the inferior oblique cut away. If the dissection is not carried too close to the origin of the recti muscles, all the muscles may be kept in their place. If the globe has not been previously hardened in formalin, the specimen can be placed in a weak solution (5 per cent.) and, at the end of 10 to 12 hours, the muscles become rigid and can be more easily studied; besides the specimen can be kept indefinitely in the solution.

**Microscopic Section Making.**

The explanations and directions given above will permit the student to investigate the gross or macroscopic appearance of the various parts of the eye. If he wishes to go farther and to study the minute structure of the various coats and media, i.e., to proceed to a study of the normal histology of the globe, he will have to proceed to a microscopic examination of thin sections of the parts under investigation.

A few remarks on microscopic section making will be useful to the student unacquainted with this kind of work.

Beside the dissecting instruments mentioned in the first part of this chapter, teasing needles (mounted on a wooden handle) are required, together with a set of reagents (the most commonly used of which will be mentioned presently) for mounting or staining the preparation. In addition to this, a good microscope, slips of clear glass termed slides on which the specimen that is being examined is placed, and small pieces of very thin glass, termed cover slips, which serve to cover the preparation are necessary.

**The Microscope.**

The microscope consists essentially of a tube carrying two systems of lenses, one at the upper end, termed the eye-piece or ocular, and one at the lower end, termed the object lens or objective.

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The stage is the perforated plate attached to the stand of the microscope and upon which the preparation is placed for examination. A mirror placed under the stage serves to reflect light up to the central aperture in the stage and along the tube of the instrument.

The tube of the microscope which carries the ocular and the objective is in some instruments moved towards or away from the stage by a rack-and-pinion arrangement. In some simpler models, it merely moves up and down by twisting it in a slightly larger tube fixed to the stand. In the latter case it should be ascertained that the microscope tube twists easily; if it does not, the tube should be thoroughly cleaned. When the tube is moved in either of the above ways, the coarse adjustment is said to be used. In good class instruments, the tube can also be moved up or down through a small amount by turning a milled head at the top or at the side of the pillar. If the milled head which works a micrometric screw is turned in the direction of the hands of a clock, it lowers the tube, i.e., brings the objective nearer to the preparation. Turning the milled head in the opposite direction raises the tube. This arrangement for raising or lowering the tube through a very small amount is termed the fine adjustment.

The magnifying power of the microscope depends on the power of the objective and on that of the ocular.

It is advisable to have at least two objectives, namely, a low-power one working at about $\frac{1}{2}$ inch (or 12.5 mms.) from the preparation on the stage, i.e., having an equivalent focal length of about $\frac{1}{2}$ inch, and a high-power one having a focal distance of about $\frac{1}{6}$ of an inch or a little over 4 mms.

Two eyepieces of different powers are also necessary. As a rule, microscope objectives are denoted by their focal length in mms. or in inches. Thus, there are objectives ranging from $1\frac{1}{4}$ inches (or approximately 32 mms.) having an initial magnification of 4, to $\frac{1}{8}$ of an inch (about 3 mms.) with an initial magnification of 60. It should be well understood that, except in very cheap models of microscopes, the objectives, especially if of high power, are never made of a single lens; they consist of a number of lenses made of different kinds of flint and crown glass, so chosen as to counteract the unavoidable defects or aberrations which would spoil the definition of the images formed. A high class objective, as those designed by Prof. Abbé, may consist of as many as five constituent lenses. The lowest lens or front lens is generally hemispherical with its flat surface turned towards the object on the stage. Of the remaining lenses those which are divergent are made from different

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kinds of flint glass, while the converging lenses are made of various kinds of crown glass, the dispersive power and the index of these constituent lenses being so chosen and the curvatures, spacing, etc., so calculated as to minimise or eliminate the effects of the spherical and chromatic aberration.

The eyepieces generally used are of the Huygenian type and with an equivalent focal length ranging from 42 mms. (giving a magnifying power of 6 diameters) to 17 mms. (giving a magnifying power of 15 diameters).

The total magnification of the microscope is the product of the initial magnification produced by the objective by that produced by the ocular. Thus, with an objective of $\frac{2}{3}$ of an inch or 16 mms. focal length, giving an initial magnification of 10 diameters used in conjunction with a 25 mms. ocular (magnification 10) the magnifying power of the microscope is $10 \times 10 = 100$. With an objective of $\frac{1}{6}$ inch or 4 mms. (initial magnification 45) and an eyepiece of 17 mms. (magnification 15) the total magnifying power of the microscope is $45 \times 15 = 675$.

Observation of a preparation with a total magnifying power of about 90 to 100 diameters or less is spoken of as an examination under low power. Magnifications of anything between 100 and 600 or 800 diameters or more are spoken of as high power.

Care should be taken to avoid lowering the objective upon the mounted specimen since this may displace the front lens of the objective out of its correct position. High powers should not be used for thick objects.

An iris diaphragm is usually fitted to the stage in order to cut peripheral rays which are not brought to the same focus as the central or axial rays. High-class microscopes are also fitted with a sub-stage condenser which serves to concentrate the light thrown up by the mirror on the centre of the preparation; this arrangement is especially valuable when high powers are used for the observation of stained sections. The sub-stage, if any, should be raised so that its upper surface is level with the stage.

We cannot, within the limits of this work, give a full account of the theory of the microscope.

It will be sufficient to say that the objective gives a real inverted image of the object on the stage. This real image can be seen as an aerial image if the microscope is fitted with a low power objective and the eyepiece is removed. On looking into the tube, the observer will see an image which is magnified 5 or 8 diameters if the objective is $1\frac{1}{4}$ or $1\frac{1}{2}$ inch focal length. The eyepiece serves to look at the

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real image formed by the objective and acts with respect to this image as a magnifying glass.

In modern instruments, the eyepiece is not made of a single convex lens, but of the combination of two plano-convex lenses, the convexity of each facing the incident light, i.e., turned downwards when the eyepiece is in position. The lower lens of the eyepiece, termed the field lens, is placed in front of the plane in which the real image formed by the object lens is located and transforms this image into another real image which is viewed through the upper lens acting as a magnifying glass and furnishes a virtual magnified image of the object under examination. This combination constitutes what is termed a Huygenian eyepiece and is especially valuable in microscopic work as it corrects more completely than any other system of lenses the aberration of the objective, which would be extremely troublesome with the high magnifying power obtained by means of the microscope.

**Conditions to be fulfilled in the Microscopic Examination of Small Objects by Transparency.**

Objects viewed with the microscope are necessarily small and, in the majority of cases, are examined by transparency. In order to be thus examined by transparency, the small object must be very thin, and in histological practice it generally consists of a thin section of a particular tissue, or a small fragment teased or dissociated in order that its constitutive elements may be readily seen. Often colouring matters or stains are used, as we shall see presently, so that the various parts of the preparation may be differentiated, some anatomical elements taking a particular stain while some others are not affected by it or at any rate are not so deeply coloured.

The section or the fragment of dissociated tissue under examination does not merely rest on the slide, but is immersed in a fluid and covered by the cover slip. Not only does this procedure protect the preparation against dessication and atmospheric dust, but it also fulfils an optical purpose. To prove this we have only to look at a small object, say, a cotton thread, first in the dry state and then when immersed in a liquid. In the first instance none of the details which are clearly made out when the object is seen immersed in a liquid can be recognised. The reason is easy to understand. When light passes through a porous structure like a bit of cotton thread, this thread contains air so that light has to pass through a solid matter separated by layers of air; hence the light suffers a series of refractions,

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reflections and scatterings, which cause changes of direction and a loss of illumination. This effect is considerably minimised when the object under examination is observed immersed in a medium the refractive index of which approximates that of the solid object itself. A simple experiment will make the matter quite clear. Let us put a glass rod in a bottle through a hole in the cork. If the bottle is filled with air the rod will be quite easily seen on a white background, and its edges may even appear dark. Now let us fill the bottle with water; the rod will become more transparent, the dark edges tending to disappear. If water is replaced by Canada balsam or by cedar oil or by any other medium, the refractive index of which differs very little or not at all from that of glass, the rod will hardly be visible or will be quite invisible. It follows that a bundle of fine glass threads will appear practically opaque in air but will become more and more transparent as it is immersed in liquids the refractive index of which approximates more and more closely that of glass itself. The same phenomenon will occur for any substance, e.g., a filament of cotton as we have already mentioned or a thin fragment of tissue from the living body. In certain fluids, these specimens will become practically transparent and to examine their minute structure, staining has to be resorted to. With careful staining, details of structure will appear which could not be made out in any other way.

Hence the importance of the choice of the liquid in which the preparation is mounted. According as the preparation is mounted in water, or in glycerine (of higher index than that of water), or in Canada balsam, a good staining will be necessary, all the more so if the index of the fluid in which the preparation is mounted approximates that of the various constituents of the preparation itself.

Most living tissues can be observed, without staining, in water or salt water. Glycerine affords a higher transparency than water, but certain details of structure will escape notice if the preparation is not properly stained. Canada balsam gives more transparency still but requires excellent methods of staining.

As we have already stated, it is a necessity to harden a globe completely before cutting it, especially if it is intended to make thin sections for microscopic examination.

**Various Processes in the Making of Microscopic Sections.**

The various processes in the making of a microscopic section are: (1) fixation, the purpose of which is to allow the different anatomical elements of a given tissue or organ

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to preserve the shape they had during life. The action of fixing media is different according to the particular medium used. For instance, some, e.g., alcohol, picric acid, act in coagulating the albumin of the tissues. Others, like bichromate of potash, enter into combination with the protoplasm of the cells; others again, like osmic acid and bichloride of mercury, are reduced in the presence of some elements of the tissues to which a metallic appearance is thus imparted.

A good fixing medium must (a) kill as rapidly as possible the anatomical elements, and keep them in the position they occupied during life; (b) allow a good optical differentiation; (c) have a sufficient penetrating power to fix the deep parts of the preparation as well as the more superficial ones; (d) cause as little distortion of the tissues as possible.

A fixing medium which was formerly very extensively used in practice is alcohol, which acts in coagulating albumin and dehydrating the tissues. Its use is, however, always accompanied by a pronounced retraction and for this reason, alcohol is now rarely used by itself. In the case of the eye, the vitreous body and still more so the retina become retracted and often torn by a too energetic fixing in alcohol. Even the sclerotic, in spite of its resisting power, is often retracted and assumes an irregular shape.

Müller's fluid, which is very often used as a fixing medium, consists of

Bichromate of potash, 2 to 2.5 grammes.
Sulphate of sodium, 1 gramme.
Distilled water, 100 grammes.

This fluid penetrates the tissues fairly quickly, but it should be renewed every day during the first week, and once or twice a week during the following period. It takes about five to six weeks to harden a whole globe.

Formol or formalin, which is an aqueous solution of formaldehyde, is a satisfactory fixing medium convenient for quick work. The commercial formalin, obtainable at any chemist, contains 40 per cent. of formaldehyde and should, before use, be diluted in the proportion of 1 of commercial formalin to 9 of water, which gives in this way a 10 per cent. solution sufficient for the purpose in view. The globe is immersed in the liquid and, to avoid the possibility of retraction and change of shape, it should rest on a pad of cotton wool at the bottom of the bottle or jar in which the fixation is carried out. A good fixation by means of formalin requires from 12 to 24 hours, according to the size of the bulb, but the latter limit should never be exceeded, as then the cornea, the sclerotic, and especially the lens would become too hard for section making.

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The next step is a thorough washing of the specimen as it is removed from the fixing fluid and its dehydratation, the purpose of which is to remove all traces of the water which may have penetrated the tissues. This dehydratation is carried out by means of the process we have already alluded to as "running through the alcohols," i.e., by immersion in alcohols of increasing strength, say, a day in alcohol at 70 per cent., a day in alcohol at 80 per cent., and a day or two in alcohol at 95 per cent., or better still, in absolute alcohol.

The specimen, for instance the whole globe, is then ready for section making. The direction in which the section is made depends of course on the portion of the globe that is being investigated. To cut a whole globe the section is often made along the antero-posterior direction passing through the corneal centre in front and through the region of the posterior pole behind. This section is, however, difficult and there is a possibility that a most interesting part of the eye (the macula) is not included in it. Moreover, the section of the eye as a whole, though often interesting and useful, always presents a difficulty owing to the fact that the various parts forming the ocular coats offer a very unequal resistance to the cutting instrument. The choroid and retina are easily cut but the sclerotic is much more resisting. Besides, when the globe is cut the lens is liable to escape from its capsule during the process of preparation. The only way to avoid these drawbacks is to cut fairly thick sections which, owing to their thickness, will not lend themselves to the microscopic examination.

In fact, antero-posterior sections should mainly be made to obtain a general view of the eye, as we have indicated in the part of this chapter devoted to dissection. To obtain such sections in the best way, the globe should be held with its antero-posterior axis horizontal and two spherical calottes are detached, one a little below the upper pole and the other slightly above the lower pole. The height of each of these calottes should be about one-fifth of the vertical diameter of the eye. It is then easy to stick one of the flat surfaces thus obtained on a piece of cork serving as a support and to make by hand sections parallel to the flat surface of the globe as it is now, commencing with the superior part and reaching gradually the papillar region.

A razor with one of its surfaces flat is a good cutting instrument, and a safety razor blade is equally satisfactory. With a little practice it is possible to obtain fairly thin sections.

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For the section of small pieces of tissue, too small to be held in the hand, the specimen is enclosed in a cylinder of pith as follows. The cylinder is cut longitudinally in two halves and the flat surface of each half is hollowed to form a cavity in which the specimen is enclosed. The two halves are then bound together by a few turns of thread below the specimen, which is thus kept in its place. Then the pith and the specimen are cut together by the razor, the various sections made being placed in a shallow vessel containing alcohol in which it becomes easy to separate the pith from the sections themselves.

**The Microtome.**

Various instruments called microtomes have been devised to make sections of extreme thinness, but such instruments are necessarily expensive and beyond the reach of the amateur.

A simple model designed by Ranvier is, however, inexpensive and useful. It consists of a hollow cylinder fitted at its upper end with a perfectly flat disc. The bottom of the cylinder consists of a plate of metal exactly fitting the inside of the cylinder and can be raised or lowered by means of a micrometric screw, one whole turn of which will raise or lower the movable bottom by a given amount, say, a quarter of a millimetre. The specimen to be cut is placed in the cylinder, the movable bottom being at its lowest position. The specimen is kept in a definite position by means of pieces of pith introduced between the specimen itself and the inner wall of the cylinder. The screw is then turned so as to raise the movable bottom together with the specimen. When the latter reaches the level of the upper plate at the superior opening of the cylinder, the razor is moved along the plate so as to give a first cut. Then the screw is turned so as to raise the specimen by, say, 1-10th mm., and a second section is made, the thickness of which will be equal to the excursion of the screw.

The microtome of Ranvier is not made of a size to take the whole of the globe, though it would not be a difficult matter to have a similar model made of the proper size. As it would be almost impossible to fix the globe in the cylinder in an absolutely steady way by means of pieces of pith, an alternative method consists in filling the cylinder with melted paraffin wax and placing the eye in the melted fluid in a position corresponding to the direction of the sections it is proposed to make. When the wax is quite set, a turning of the screw will ultimately bring the globe level with the



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terminal plate of the cylinder and slightly above it. Then a first section is made. The screw is turned again a little to push the globe upwards, and further sections are made.

**Embedding of the Globe in Celloidin.**

An alternative to the above method and easier to use is the embedding of the globe in celloidin. The globe should be thoroughly dehydrated by being immersed in alcohols of increasing strength as stated before. If this is properly done, better results will be obtained with the simplest cutting apparatus than with the most complicated microtome. Celloidin is procurable in the form of soft, semi-transparent tablets or shavings. These pieces are well dried until they acquire an amber colour and can then be kept in well-corked bottles. A thin solution is obtained by dissolving ten grammes of celloidin in a mixture of 120 cubic centimetres of ether and 120 cubic centimetres of absolute alcohol. This solution is usually called the thin solution. To obtain a thicker one 10 grammes of celloidin are dissolved in a mixture of 60 cubic centimetres of ether and 60 cubic centimetres of alcohol.

After hardening the globe is placed first for a few days (5 or 6) in a mixture in equal proportion of alcohol and ether, then for about 8 days in a thin solution of celloidin, and finally for a similar period in thick celloidin. The celloidin penetrates the tissues of the eye and gives them a consistence which permits of an easy cutting.

The globe, cut as we have stated above, is then stuck on a piece of wood or on a piece of cork, but it is necessary to avoid the use of wood or cork which has not previously been placed for a fairly long time in alcohol at 70 per cent.; otherwise the colouring matter contained in the wood might be diffused in the celloidin and in the preparation.

The fixing of the globe to its support is quite a simple matter. The piece of wood or cork is coated with a layer of thick celloidin and the globe pressed against it for a few minutes. Should the globe not be required for immediate cutting it can be kept in alcohol. A specimen stuck with celloidin should never be kept in the atmosphere as it would become distorted and unusable after a few hours.

The globe can then be cut either by hand by means of an ordinary razor, or by a safety razor blade, or again, in a microtome. With some practice, sections of a thickness of 20 microns are obtainable. The sections which remain on the blade are collected with a camel-hair brush wetted with alcohol at 90 per cent., and are transferred into a vessel full of alcohol.

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**Staining.**

The staining of the section is the next step. We cannot give here full details of this important part in the work of the microscopist, and refer the student to more complete books on the subject.

For our present purpose it will be sufficient to say that the general arrangement of the cells in a tissue is brought out by staining the nuclei of the cells. For this, a basic stain is used such as hematoxylin or basic fuchsin. Both stains contain other constituents to a variable extent. By special treatment, the stain can be more or less completely confined to the nucleus.

In order to make out other elements of the tissue in addition to the nuclei the sections, after having been stained with hematoxylin or basic fuchsin, are stained with an acid stain, commonly eosin and Van Gieson fluid (a mixture of acid fuchsin and picric acid).

Eosin and picric acid stains colour the cell substances diffusely; both stain red blood corpuscles deeply if, as is the case with most fixing agents, the hemoglobin has been preserved. Eosin stains them orange, picric acid yellow. White fibrous tissues are coloured deep red by acid fuchsin stains.

When the sections have been stained, as we shall explain in dealing briefly with the various parts of the eye, it remains to mount them to protect them from the action of the atmosphere and to give them the necessary transparency. As we have already remarked, the specimens examined under the microscope should be placed in a medium the refractive index of which is adapted to their degree of transparency; this medium must be able to penetrate the tissues under examination and should be such that it conserves the various constituents of these tissues in the state they were during life and protects them against putrefaction or other chemical changes.

Objects of some thickness or which have a certain natural opacity should be mounted in a medium of a high refractive index, approximating that of glass (e.g., Canada balsam). The necessity for this is that the whole of the preparation must, as far as possible, represent a medium of uniform index. In the case of fine objects fairly transparent and colourless, the details of which would be lost in the abundant light transmitted through the microscope, less refringent mounting media (water, albumin, gelatine, etc.) are advisable, as they moderate the amount of light entering the object lens and thus place the objects in more favourable conditions of visibility.

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In practice, though many media fulfil the required condition, only two kinds are generally used, namely, various resins and glycerine.

Resins are transparent substances soluble in chloroform, xylol, and essential oils, but insoluble in water, and precipitated by alcohol in the form of a white deposit. The resins usually used in histology are Canada balsam and Dammar resin.

Canada balsam is employed in solution in xylol or in chloroform and is especially useful for the mounting of preparations containing fats stained by osmic acid or by substances which would become colourless in the ordinary commercial xylol. Dammar resin is dissolved in turpentine oil or in benzine.

Whether Canada balsam or Dammar resin is used, the solution must be transparent and of such a fluidity that, if it is taken by means of a glass rod, the drops from it gently fall off one after another without being elongated in a filament. If this fluidity were disappearing by evaporation of the solvent, it should be obtained again by addition of a few drops of the substance in which the resin has been dissolved.

The employment of a resin as refringent and preserving medium involves a series of four separate operations, namely, (a) dehydratation, (b) penetration, (c) washing, and (d) final mounting.

(a) Any specimen which has to be mounted in a resin should be thoroughly dehydrated by successive immersions in alcohol of increasing strengths from about 70 per cent. to begin with to absolute alcohol to complete the work. An incomplete dehydration would prevent a section from being well impregnated with the resin in the following steps and would cause it to become more or less distorted. A final immersion in alcohol for a period of a few minutes is a necessary condition.

(b) The dehydrated sections cannot be placed at once in the resin as the alcohol they are impregnated with would precipitate the resin. They must be placed for a few minutes in a fluid which will substitute itself for the alcohol and will be readily mixed with the resin. Xylol or essential oils (e.g., oil of cloves, or oil of bergamot) are most frequently used for this purpose. Oil of cloves has the property of remaining on a plate of glass in the form of a drop without being spread into a film; it easily bathes and penetrates the preparation on which it is placed, but it has the drawback of discolouring sections, especially those stained with eosin

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or other aniline dyes. When this drawback is of importance, the oil of cloves should be replaced by xylol or even by chloroform.

(c) When the section is well dehydrated and impregnated with xylol or with oil of cloves, or with chloroform, a few drops of Canada balsam are poured over it; not only does this substance penetrate the tissues, but it appreciably increases the transparency of the preparation and may for this reason be regarded as a clearing medium.

(d) The mounting of the preparation is completed by placing over it on the slide a cover glass on the lower surface of which a drop of Canada balsam is applied. A slight pressure will spread the drop and eliminate the bubbles of air which would prevent a good view under the microscope. On drying, the Canada balsam becomes solid and maintains the contact between the slide carrying the preparation and the cover slip. Preparations thus mounted in Canada balsam can be kept for very long periods. Should the preparation be mounted in glycerine, the method is somewhat simpler. A previous dehydratation is not so necessary and the section placed on the slide may be at once covered with a small drop of glycerine. The cover slip is then applied as before, but it has to be cemented to the slide by means of paraffin wax, or of ordinary wax, or again, of a little Canada balsam.

**Examination of Simple Objects under the Microscope.**

These preliminary explanations being understood, we would suggest that the student who is not acquainted with microscopic work begins with the examination of simple objects, such as starch granules, air bubbles, linen, cotton and woollen fibres, as well as the usual constituents of the dust of a room.

To examine starch granules, gently scrape the cut surface of a potato with a knife; shake the starch granules thus obtained into a drop of water on a clean slide, and apply a cover glass on the preparation. With a low power, the granules appear like dark specks of variable sizes; under a high power, they are seen as clear, flat, ovoid particles with a sharp outline. The change in appearance of the outline as the microscope is focussed up or down should be observed. On close examination, fine concentric lines are to be seen around a minute spot which is usually placed excentrically near the smaller end of the granule.

The appearance of air bubbles in water should be carefully noted; if comparatively large, they are clear in the

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centre with a broad dark border due to the refraction of light. If small they may look entirely dark.

The examination of brewer's yeast which has been grown in a solution of sugar is interesting. Observe the yeast particles, some of which are budding. Each particle contains a clear vacuole and has a well-defined outline due to an external membrane, a feature which does not generally occur in animal cells.

Some mould (or Penicillium) examined in water will show the long branching filaments and also the spores or cell particles from which in some instances the filaments are sprouting.

Fibres of cotton and of linen viewed in water under a high power will show distinctly the difference between the well defined, relatively coarse, and slightly twisted fibres of linen and the longer, thinner and more twisted cotton fibres.

Mount two or three hairs of the head in water and look at these with the low, then with a higher power. Examine also some fibres of woollen material and compare them with the hairs. They have very much the same structure though the wool fibres are finer and more curled.

An examination of dust collected on a slide, immersed in a drop of water and viewed with a high power will show, in addition to numerous black particles of carbon (soot), a quantity of fibres of linen, cotton, or wool, as well as shreds of epithelial cells derived from the epidermis.

The observation of the amœba, a microscopic unicellular being, has been alluded to in page 14.

**Measurement of the Actual Size of Objects Viewed under the Microscope.**

It is advisable in microscopic work to have a means of ascertaining the actual size of the objects viewed. To do so, a stage-micrometer (i.e., a slide ruled in the centre with lines 1-10th or 1-100th mm. apart) is placed under the microscope in such a manner that the dividing lines run from left to right. These lines are focussed as well as possible by means of the coarse adjustment and their definition is improved by the use of the fine adjustment of the microscope if the instrument is fitted with one. A piece of white cardboard is then placed on the table on the right side of the microscope. On looking through the instrument with the left eye and keeping the right eye open, the images of the lines seen through the microscope will appear projected on the cardboard. Their apparent distance is marked with a pencil on the cardboard and afterwards a scale of lines

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is drawn in ink at the same intervals. A magnified reproduction of the micrometer is thus obtained. Mark upon the cardboard the number of the objective and that of the eyepiece used, as well as the length of the tube of the microscope. This scale card will serve the measurement of any object without further use of the micrometer. To measure an object, place it on the stage of the microscope and place the scale card on the table on the right of the microscope. Look at the object with the left eye and keep the right eye open. The object will then appear projected on the card and its size in tenths or hundredths of a millimetre can be read off. It is, of course, necessary to have a special scale card made for any combination of object lens and eyepiece that is being used and also that the tube length of the microscope be the same.[1] The lines on English made stage micrometers are usually ruled 1-100th and 1-1,000th of an inch apart (i.e., $\frac{1}{4}$ and $\frac{1}{40}$ of a millimetre).

There are other methods for the measurement of the apparent size of microscopic objects, for which we refer the student to more complete works on microscopy, but the above method is very simple and quite sufficient for ordinary purposes.

To complete these brief explanations on the subject of microscopic examination generally we must give a few details on the examination and preparation of the various tissues constituting the eye.

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[1] It is easy to understand, from what has been said above, that the magnification obtained with a microscope depends on the proper choice of the objective and of the ocular or eyepiece. Most objectives permit the use of an eyepiece of as high a magnifying power as 15 diameters but in practice a magnifying power above 10 diameters by means of the eyepiece should not be used. It is a matter of experience to select the objective and the eyepiece required to give a particular total magnifying power, but as a rule it is not advisable to use a high power eyepiece with a weak objective and conversely.

It is possible to increase the magnifying power produced by a microscope fitted with a given objective and a given ocular. This can be done by extending the tube of the instrument. Manufacturers call "tube length of a microscope" the distance from the eye lens of the ocular at the top end of the instrument to the point where the objective is screwed in at the lower part of the tube. British made microscopes have a tube length of 140 mms., but good class instruments are fitted with what is termed a sliding draw tube which enables the observer to increase the tube-length from 140 to 200 mms. For a given set of objectives and eyepieces, the total extension of the draw tube from 140 to 200 mms. causes an increase of magnifying power equal to about half as much as the original magnification obtained when the tube length is at its minimum value of 140 mms. Thus if the magnification with the tube length of 140 mms. is 300 diameters, the total extension of the draw tube will raise it to about 450 diameters. A smaller extension of the draw tube will cause a smaller increase in the initial magnification. A graduation engraved on the draw tube permits of two successive examinations to be carried out with the same magnifying power. Of course, the extension of the tube length requires a new focussing of the preparation under examination.

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It should be quite understood that we can only describe the simplest methods used in this kind of work, i.e., those methods which can be made use of without any elaborate material.

**Microscopic Examination of the Lids.**

As already pointed out, each lid is a complex structure in which many various histological elements can be made out. The external surface of each lid is covered by ordinary skin, while the surface close to the eyeball is lined with the mucous membrane we have described under the heading of conjunctiva. The lids contain striated or voluntary muscular fibres, plain or unstriped or involuntary muscular fibres, dense fibrous tissue or tarsal cartilage, fat, hairs, glands, nerves, blood- and lymphatic vessels. The relations of these parts to each other are best studied in a vertical or sagittal section cut in a direction at right angles to that of the free margin, though sections in other directions may be useful to elucidate some points of structure.

To prepare a lid for section, it should be hardened in alcohol or formalin and the sections when made in the direction stated above are stained with hematoxylin[1] and mounted in Canada balsam. The outline of a vertical section of the whole upper lid is long and narrow, the slightly curved surfaces running from the ciliary border more or less parallel to one another till about the orbital margin of the tarsus where they begin to diverge, the conjunctival surface bending inwards towards the upper fornix. The outline of a vertical section of the lower lid is shorter, thicker and assumes the shape of a wedge, since the two surfaces form an appreciable angle at the junction of the outer skin and of the conjunctiva.

The long sacculated Meibomian glands will be quite apparent as they lie in the dense connective tissue (the tarsal tissue) close to the conjunctival surface, their ducts opening at the posterior part of the lid's margin. External to these the bundles of fibres of the orbicularis muscle will be seen cut across; a few of the fibres of the muscle lie on the conjunctival side of the ducts of the Meibomian glands.

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[1] Hematoxylin, sometimes spelt Hæmatoxylin, is the colouring matter of Logwood. In the dry state, it appears as a light-brown powder soluble in alcohol. The solution generally used in practice consists of:—

| | | |
|---|---|---|
| Distilled Water | .. | 100 c.cms. |
| Absolute Alcohol | .. | 100 c.cms. |
| Glycerine | .. .. | 100 c.cms. |
| Glacial Acetic Acid | .. | 10 c.cms. |
| Hematoxylin | .. .. | 2 grammes. |
| Alum | .. .. .. | to saturation. |

The mixture is exposed to light until it assumes a deep red colour when it constitutes a stable stain, which can be kept for a long time in a well-corked bottle.

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A short distance from the Meibomian glands fairly large sebaceous glands are seen and outside these the eyelashes are inserted. In the outside layer of the fine skin which lines the lid externally, a few small hairs may be seen. Towards the canthi some small bundles of involuntary muscular fibres (Müller's muscle) may be seen, cut longitudinally on the section. In the upper lid the fibrous attachment of the levator muscle may be observed attached to the dense connective tissue or tarsus. The palpebral conjunctiva is intimately united to the tarsus, at least on the greater part of the inner surface of the lids, but in the region of the fornices the conjunctiva is much looser and is thrown into horizontal folds, the purpose of which is to allow a free rotation of the globe in its socket.

The lachrymal gland may be briefly mentioned in connection with the lids. It is a compound racemose gland yielding a watery fluid. Its ducts, of which there are several, as we have seen before, open on the conjunctival surface in the upper fornix near the outer canthus.

**Sections of the Whole Globe.**

The most convenient way of cutting sections of a globe for the purpose of microscopic examination is probably the method of celloidin embedding we have briefly described (page 386). As a preliminary step, sections through the posterior hemisphere of an eyeball that has been hardened in Müller's fluid or in formalin are stained and mounted in the usual way, and are useful to show the relative thickness of the various coats and the layers of which these coats are made. Sections passing through the point of entrance of the optic nerve will exhibit the manner in which the nerve fibres pierce the outer tunics and reach the retinal surface. The modifications which are found in the neighbourhood of the fovea centralis, and have been described (page 247) may also be made out if the section has been cut in a human eye.

Sections of the anterior half of an eyeball that has been hardened in Müller's fluid or in formalin should pass through the middle of the cornea; the lens may be left *in situ*, but this complicates the process of section-making and the mounting of the preparation on account of the extreme hardness of the lens tissue. The celloidin method of embedding is easier. The specimen under investigation is thoroughly dehydrated by running it through the alcohols and is then placed in a solution of celloidin in alcohol and ether as previously stated. After twenty-four hours, it is removed from the celloidin solution and placed upon a flat wooden holder. When the celloidin is set, the holder is immersed in alcohol

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80 per cent., and after a few hours, sections are easily cut with a razor or a safety razor blade wetted with alcohol of the same strength. The main advantage of this method is that the celloidin which has penetrated the globe, and is quite transparent, need not be got rid of in mounting the sections and serves to keep together in their normal relationship the various constituents of the specimen under investigation. The method, for this reason, is particularly useful for friable tissues or for large sections. The specimen under investigation may be stained in bulk before embedding or the sections themselves may be stained after they are cut.

In studying transversal sections of the anterior hemisphere of the globe, a general sketch should be made under a low power to ascertain the relations of the various parts. The layers of the cornea, the junction of the cornea and sclerotic, the ciliary muscle, the iris and the mode of suspension of the lens as well as the arrangement of the pars ciliaris retinæ can be easily ascertained.

**Sections of the Cornea.**

A tangential section of the cornea stained with gold chloride[1] should be made and the student should sketch three or four of the connective tissue cells or corneal corpuscles. The distribution of the nerve fibres and their termination amongst the corneal epithelial cells, which have previously been described, are clearly shown in a chloride of gold preparation.

A section of cornea stained with nitrate of silver[2] will show the branched cell spaces corresponding to the connective tissue cells of the previous preparation.

The latter preparation is best made by rubbing the corneal surface with lunar caustic after scraping off the epithelium. In ten to fifteen minutes, by which time the lunar caustic (i.e., the nitrate of silver) will have penetrated the thickness of the cornea, the eye is carefully washed out in distilled water and exposed to light, when tangential sections are made, for which purpose the cornea may be hardened in alcohol.

[1] Gold chloride is a yellow salt usually obtainable in small tubes containing one gramme of it in solid form. It is used in solution in distilled water in the proportion of one part of the salt for one hundred parts of water.

[2] Silver nitrate is obtainable in the form of crystals and is used in aqueous solution at 1% made with distilled water. (It is imperative not to use tap water for the purpose as this always contains a slight proportion of salt which would cause the nitrate of silver to be precipitated in the form of insoluble silver chloride.) The solution keeps fairly well in the dark and should be stored in blue or brown bottles with a glass stopper. If a solution of a weaker strength is required, it can easily be made by diluting the 1% standard solution with the proper amount of distilled water.

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A vertical section of the cornea, made near the margin, shows clearly the arrangement of layers we have described in page 162. The stratified external epithelium, continuous with the epithelium of the conjunctiva, is followed inwards by the thin lamina of homogeneous connective tissue termed Bowman's membrane upon which the deepest cells of the epithelium rest. Then comes a thick layer of connective tissue forming the true corneal substance. It is continuous laterally with the tissue of the sclerotic and is made of fibres arranged in regular laminæ, the directions of the fibres crossing one another at right angles in the alternate laminæ.

The anterior corneal epithelium is made of a superficial layer of flattened cells, then an intermediate layer of rounded or polygonal cells the edges of which are serrated in order that each cell may fit in the neighbouring one. The most internal layer of the epithelium consists of high cylindrical cells, the bases of which rest on the next corneal stratum, i.e., on Bowman's membrane. The latter is stained a vivid pink with picro-carmine.[1] The next corneal layer, constituting the greater part of the corneal thickness, is the substantia propria formed of connective tissue fibres arranged in superimposed laminæ which remain colourless when the preparation is stained by hematoxylin but stain a deep pink with picro-carmine.

Between the lamellæ of the substantia propria we can observe numerous oblique bundles of fibres which give the preparation, especially if mounted in glycerine, the appearance of a glassy mass with cracks or spaces lodging cells united to each other by processes bathing in the lymph circulating in the spaces. Descemet's membrane, the next corneal layer, is coloured in yellow orange by the picro-carmine which shows that this layer has thus colouring affinities differing from those of Bowman's membrane. Descemet's membrane is a thin glassy structure becoming

[1] Carmine is a coloured body derived from the insect called Cochineal. It occurs in the form of irregular fragments of red colour. The kind most useful for microscopic work is known in the trade under the name of Carmine No. 40. It is practically insoluble in water or in alcohol but readily soluble in ammonia. When, however, it is mixed with alum or with borax, it can be dissolved in hot water or in hot alcohol and forms an excellent stain. Thus, 1 gramme of Carmine No. 40 and 5 grammes of Alum are dissolved in boiling water, the boiling being continued until the mixture becomes of a deep violet-red. This solution, which is called Alum-Carmine can be kept for a long time if a few crystals of camphor or of thymol are placed in it to prevent the formation of fungi.

The picro-carmine solution is obtained as follows:—In a porcelain dish, containing a saturated solution of Carmine in ammonia, a solution of picric acid in water is added. The mixture is heated, when the ammonia partly evaporates and the remaining liquid assumes a characteristic blood-red colour. This is filtered and should be kept in well stoppered bottles.

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thicker with age and offering a great resistance to the process of ulceration which so often affects the cornea. When cut or ruptured the edges have a tendency to curl up like all elastic structures.

The innermost corneal layer is the endothelium which lines Descemet's membrane and is made of a few layers of epithelial cells with a nucleus projecting towards the anterior chamber. In fact, Descemet's membrane is a product of the secretion of these cells.

For the microscopic examination of the cornea, fixation in formol for about 12 hours is satisfactory. Then a double staining by hematoxylin and eosin[1] or picro-carmine is advisable. The fundamental tissue is coloured pink in either case and the fixed cells appear with clearness.

**Sections of the Uveal Tract.**

The sclerotic being removed from the anterior part of a globe preserved and hardened in Müller's fluid, shreds from the choroidal surface, including amongst them portions of the ciliary muscle, are detached, stained with hematoxylin and mounted in Farrant's fluid, i.e., in a mixture of glycerine and gum. The branched pigment cells of the choroid, the elastic network and the mode of attachment of the ciliary muscle will then be quite clear.

A further interesting preparation, though a more difficult one, consists in injecting the choroid and iris. A portion of the choroid and iris is mounted in Canada balsam after a coloured solution has been injected into the blood-vessels to show their distribution more plainly. The process is not easy. The material used for injection may be a solution of

[1] Chemically, eosin is a tetrachloride of fluorescein and constitutes an acid dye obtained by the action of bromine on fluorescein suspended in glacial acetic acid. Fluorescein itself (or uranin, as it is sometimes called) is a substance produced by heating phthalic anhydride with resorcine. It has the appearance of a brownish powder readily soluble in water: the solution is of a beautiful fluorescent green; it has a certain though fugitive dyeing power and is most useful in eye work to detect slight abrasions of the cornea. The dye fixes itself on any part of this membrane in which the epithelium is destroyed and such parts assume therefore a greenish fluorescent colour. The method is extremely useful for the diagnosis of corneal abrasions or ulcerations of such a small size that they might escape observation in the most careful examination by focal illumination.

The eosin used in microscopic work is in the form of a reddish powder: there are two kinds on the market, one which is soluble in alcohol and is often called eosin-primrose, while the other kind is soluble in water.

A solution of eosin-primrose is made of 0.25 grammes of eosin in 100 c.cms. of absolute alcohol. It is of a vivid red when seen by transmitted light and shows a marked fluorescence when seen by reflected light. The other kind of eosin is also fluorescent when dissolved in water though to a less extent than the former. The solution generally used in practice is made of 0.5 grammes of eosin for 100 c.cms. of distilled water.

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gelatine in which the colouring matter, usually red, is suspended; this is injected into a blood-vessel by means of a syringe under uniform but not too high pressure in order to avoid a rupture of the vascular walls. The gelatine, which is used in a warm condition, solidifies on cooling. A simpler way consists in using a cold solution of carmine made of 1 gramme of carmine dissolved in a little water containing about 15 drops of concentrated ammonia and afterwards diluted with 20 c.cms. of glycerine. To this is added a mixture of 30 c.cms. of glycerine and one gramme of ordinary salt. The whole is diluted with an equal quantity of water. The cold process of injection described just now applies very well to the demonstration of the lymph spaces of the cornea. The pointed canule of an ordinary hypodermic syringe is pushed into the tissue to be injected and it is left to chance to determine what spaces are opened. The injection is performed under a low and constant pressure.

Another way equally well adapted to the demonstration of the corneal lymphatic spaces is the use of Berlin blue injected in solution into the posterior layers of the cornea. This stain has the advantage of not staining the corneal tissue. Tangential sections should be made from the back of the cornea.

**Microscopic Examination of the Iris and of the Choroid.**

To examine the iris, the best way is to cut the anterior segment of the eye along the equator, fix it in formol and dehydrate it in alcohols of increasing strength. The iris, being thus fixed and hardened, is detached with a pair of scissors at the ciliary insertion. Staining with carmine is the best as the coloration stands better in contrast with the pigment than would be the case if hematoxylin were used.

It will then become apparent that from the anterior surface inwards, the following layers are recognised:—

(1) An epithelial layer made of flattened cells.
(2) A layer of connective cells tightly packed and ensheathed in a thin membrane of supporting tissue.
(3) A stratum of vascular and connective tissue in which the blood-vessels of the iris are contained (iris stroma).
(4) A thin layer, more or less pigmented, constituting the posterior limiting membrane, or membrane of Henle.
(5) A double pigmented layer corresponding, the anterior lamina to the retinal hexagonal epithelium, the posterior one to the rest of the retina deprived of its nervous elements (pars iridica retinæ).

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It should be remembered that there are, in the anterior surface of the iris, and especially round the pupillary aperture, numerous depressions we have described under the heading of crypts. Immediately around the border of the pupil, in the posterior part of the stroma, we find the smooth muscular fibres forming the sphincter of the iris. The dilator of the iris, in the posterior limiting membrane, has already been mentioned (page 188).

The structure of the choroid has been fully described (pages 174 to 186). To ascertain this structure by microscopic examination a hardened globe is cut transversely and it will generally be found that in the posterior half the retina is more or less detached from the subjacent choroid by the action of the fixing medium used. It is then easy to peel off the choroid from the sclerotic by means of a pair of scissors cutting through what we have termed the supra-choroidal membrane.

Large fragments of the choroid are thus isolated, hardened and dehydrated in alcohol and cut after embedding in celloidin. The coloration by means of carmine is the most satisfactory one. Mounting in either glycerine or Canada balsam completes the preparation. As already stated, the pigment epithelium of the retina generally remains attached to the choroid when an attempt is made to separate the two membranes. In the human eye it is easy to obtain a front view of the choroid by cutting with a pair of scissors about a square centimetre on the posterior hemisphere of the globe. Exerting a slight traction on the retina with a pair of fine forceps, the latter membrane slides over the choroid and can be easily detached. The choroid is then separated from the sclerotic by cutting with scissors the loose tissue which connects the two structures. The fragment of choroid is then placed on a slide with the retinal surface of the choroid turned upwards; dehydratation is carried out by alcohol in the ordinary way, and the preparation is mounted in Canada balsam after an application of xylol, which serves to increase the transparency of the specimen.

If the eye used is not a fresh one the pigment epithelium of the retina is more easily removed from the choroid than in the fresh state in which the two structures adhere intimately. The migration of the retinal pigment in various pathological processes is one of the most interesting facts in ocular histology. This pigment assumes the form of fine elements which move most easily in the tissue. In pigmentary retinitis this pigment is diffused along the retinal vessels, from the periphery towards the centre of the fundus.

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To obtain a general view of the zonule, a globe well hardened is cut along the equatorial diameter and the vitreous removed with a camel-hair brush from the anterior segment. Then a section is made circularly in front of the sclero-corneal margin, about level with the root of the iris. The latter is cut off and the anterior segment, viewed by transparency, will show the path of the zonule fibres extending from the ciliary processes to the lens surface.

After death alterations appear very quickly in the zonule and for this reason the best specimens to study this part of the globe are human eyeballs enucleated because of an irido-cyclitis or animals' eyes freshly removed. Hardening of the anterior segment is carried out by means of formol and this operation is followed by embedding in celloidin.

Sections are made in the ordinary way and generally in a meridional direction. However, oblique sections directed from outside inwards and from the front backwards, cross almost perpendicularly the axes of the ciliary processes and are useful to show the relation of the zonule fibres with the valleys or depressions between the ciliary processes. A convenient stain is hematoxylin and carmine.

**Section of the Whole of the Anterior Segment of the Globe to show the Ciliary Body and the Filtration Angle.**

A study of the whole anterior segment of the eye is necessary if one wishes to examine the filtration angle and the canal of Schlemm. (A somewhat diagrammatic view of this portion of the eye is given in fig. 21.) The whole of the segment should be embedded in celloidin and it is imperative that the anterior chamber be well permeated by this medium; otherwise the cornea is no longer maintained in its proper shape especially on its posterior surface, and there is a risk of it becoming folded or plaited in the process of section cutting. Hence the necessity of keeping the anterior segment in weak or thin celloidin for a long time. The section should be made with precaution to avoid the lens escaping from its capsule.

The anterior segment may be cut in two ways. The direction of section may be that of a frontal plane passing through the equator of the lens, a method which is convenient to obtain a general view of the zonule of Zinn. Or again, the sections are directed in planes parallel to the antero-posterior diameter of the globe either horizontally or vertically. It should be remembered that it is possible to distinguish these two directions on the anterior part of the globe since the corneal margin is not exactly circular but has

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the shape of an ellipse with its long axis horizontal. As a rule, it is preferable to orient the section along the vertical diameter. A good knowledge of the anatomy of the iridic angle (see page 200) is necessary to understand the process of filtration of the aqueous fluid and the mechanism of the production of a glaucomatous condition. In most operations in which an incision of the cornea is necessary (cataract extraction, iridectomy, etc.) this incision is made in the neighbourhood of the sclero-corneal margin.

The trabecular structure of the iridic angle may be studied on vertical sections of the anterior segment of the globe which show distinctly the relation of the spaces of Fontana with the canal of Schlemm.

**Section of the Retina.**

The retina is, as we have stated before, a thin membrane averaging about 0.3 mms. in thickness which lines the whole internal surface of the uveal coat but does not contain any nervous elements, and is therefore insensitive to light in the portion extending in front of the ora serrata. The optical or physiological retina, i.e., the part behind the ora serrata, is simply applied to the subjacent choroid, the only firm attachments being at the level of the ora serrata itself and around the optic disc. On the other hand, the retina normally adheres to the vitreous, and any separation between the two is of pathological nature or the result of post-mortem changes.

In dissecting the posterior segment of an eye great care should be taken to avoid a detachment of the retina from the subjacent choroid and the consequent plaiting or folding of the former membrane which would render it useless for microscopic examination.

The retina is absolutely transparent when examined *in situ* very shortly after death but, in a few hours, it assumes an opaque condition which does not permit a view of the pigmented subjacent part. Only the ciliary part (pars ciliaris retinæ) remains transparent for a longer period because it does not contain any nervous elements and because it is the alteration of these elements which produce the post-mortem opacification. These alterations are mainly due to the swelling of the innermost retinal layers and since the macula, with its fovea centralis, is the part where the nervous elements are more numerous, it is obvious that this part is first affected by the post-mortem changes. Owing to the swelling alluded to just now, a fold soon appears which extends from the macula to the disc and was called by the older anatomists the central fold of the

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retina (plica centralis retinæ). It is easy to ascertain that immediately after death the macula is perfectly transparent, at least, so long as it is viewed on its natural choroidal background. Soon, however, it assumes a yellowish tint which has led to the name of yellow spot. Recent researches have shown that if the macula does not appear yellow on a retina that is still transparent, it is because its very transparency permits a view of the subjacent choroid which greatly masks the yellow of the macula. On detaching a retina and placing it on a sheet of clear glass, the yellow spot is clearly visible; its coloration is not, therefore, due to a post-mortem change but occurs normally in the living eye.

The appearance of the retina alters more rapidly after death or when it is removed from a freshly enucleated eye than that of any other tissue in the body. This alteration is already well marked half an hour after death as shown by the greyish tint of the retina if an ophthalmoscopic examination is then performed. To study the structure of the normal retina, it is necessary, therefore, to use normal eyes removed from the living subject, a thing that is only possible in cases of enucleation performed in view of the removal of a malignant orbital tumour.

The minute structure of the retina has been studied at some length (see page 227 and after). A preliminary examination of the details of construction is made by teasing in a drop of glycerine a minute fragment of retina which has been placed for two or three hours in a 1 per cent. solution of osmic acid[1] and has subsequently been kept in diluted

[1] Osmic acid is obtainable in the form of yellow crystals generally sold in sealed glass tubes containing either one gramme or half a gramme of it. To make a solution, the best way is to remove carefully the label of the sealed tube as it is obtained from the chemist, to wash its outside very carefully in order to remove all traces of gum or paste and to dry it with a clean piece of white rag. Then the tube is held over a sheet of paper in order to collect the crystals if it were accidentally broken. By means of a file, the sealed end of the tube (supposed to contain one gramme of osmic acid) is cut off and the tube, together with its contents, is placed in a tumbler containing 100 grammes of distilled water. The time required for complete solution may be as much as two or three days, and as osmic acid is easily reduced and becomes black in the presence of organic dust and also under the influence of light, it is imperative that the above operations be carried out in an atmosphere as free from dust as possible and in comparative darkness; it is for this reason that it is advisable to use a yellow coloured glass tumbler to make the solution. Even in the best circumstances, a certain amount of reduction is unavoidable and, therefore, it is well to make the solution in small quantities and to keep it in the dark in well stoppered bottles of yellow glass.

In handling osmic acid solutions, the operator should be careful not to breathe the vapour, which is very poisonous.

Pure osmic acid in solution is usually employed for fixing the retinal elements, especially the rods and cones.



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glycerine till it is required. The separation of the retinal elements is completed by gently tapping the cover glass. It is then possible to observe and to draw, under a high power, the isolated retinal elements, namely, the rods and cones with their attached fibres and nuclei, the outer corpuscles, the inner corpuscles, the hexagonal pigment cells, the fibres of Müller, etc.

A transversal section through the posterior part of the eye of a mammal, hardened in Müller's fluid, stained in bulk with hematoxylin and eosin and embedded in celloidin will enable the observer to recognise under a magnification of about 300 diameters (a) the layer of optic nerve fibres, which is thin and inconspicuous, the fibres being without a medullary sheath; (b) the ganglionic cell layer consisting of a single layer of large nerve cells with conspicuous nuclei; (c) the inner molecular layer appearing as a very close plexus of fine fibrils; (d) the inner nuclear or inner corpuscular layer showing two to four rows of cells (bipolar cells) with round or oval nuclei; the cell substance is inconspicuous, but the nuclei are well marked; (e) the outer molecular layer, a thin plexiform layer resembling the inner molecular layer; (f) the outer nuclear or outer corpuscular layer in which the bodies of the cells are more numerous than in the inner nuclear layer while the nuclei of these cells are smaller; (g) the layer of rods and cones in which the outer and inner limbs of the rods can be distinguished. The cones will be seen to be shorter and less numerous than the rods, except, of course, in the foveal region if the examination is made on a human eye; (h) the layer of hexagonal pigment cells the inner protoplasmic processes of which envelop the free or outer end of the rods and cones. The supporting fibres (Müller's fibres) will also be seen as lines stretching from the so-called inner limiting membrane to the so-called outer limiting membrane. It should not be forgotten, however, that the two limiting membranes are not true retinal layers; they are seen on the preparation as fairly well defined lines, the inner one marking the inner boundary of the layer of optic nerve fibres and the outer one forming the apparent separation of the layer of rods and cones and of the outer nuclear layer. As already pointed out, these lines or these apparently limiting membranes are merely formed by the cut ends of the supporting Müller's fibres.

A further examination can be made as follows:—The eye of a freshly killed frog is cut out. Holding it up by the optic nerve, cut off a small part (0.5 to 1 mm.) of the ocular coats around the optic nerve. The point of a pair of fine scissors is then inserted into the holes thus made and two

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radial cuts are made including about one-third of the globe between them. The anterior part of the globe is cut off and the posterior part is placed, inner surface downwards, on a slide between two strips of fairly thick paper. The sclerotic is then removed, fixing the pigment epithelium layer at one edge and the rest of the retina at the other; the two are then pulled apart. If this is done quickly the retina will be seen of a purplish red colour due to the visual purple of the rods. The preparation is covered with a cover glass having on it a drop of Ringer's fluid (i.e., a solution of chloride of sodium, chloride of potassium and chloride of calcium in distilled water, the proportion of the three salts being 0.65 per cent. for the first and 0.025 per cent. for each of the other two. This solution, often termed salt solution, has nearly the same composition as the fluid or serum normally bathing the living tissue). An immediate examination of the preparation will show the mosaic formed by the ends of the rods and cones; most of the rods are purplish red but the colour soon fades. When this has occurred, the strips of paper are removed and the piece of retina is teased out by means of teasing needles when the large outer limbs of the rods, their longitudinal fluting and their transversal breaking into discs can be observed. A similar preparation of the retina of a mammal will show that the diameter of the rods and cones is appreciably smaller.

The pigment epithelium layer of a sheep's eye is easily studied. A small piece of retina is removed from a globe preserved in Müller's fluid. It will probably be found that the pigment epithelium layer will be left adhering to the choroid. A small piece of this layer is mounted in glycerine (or if the eye used is a fresh eye, it is mounted in the salt solution referred to just now). The microscope will show the single layer of hexagonal cells with large pigment granules.

The various preparations of the retina we have just described certainly give an idea of the complex structure of the nervous membrane of the eye, but they do not show satisfactorily the relations of the various layers. To ascertain the physiological connection between a rod or a cone on one hand, and an optic nerve fibre on the other, the retina should be prepared according to Golgi's method modified by Cajal. This method is, however, too complicated to be described in detail. What we have said (page 229) is sufficient to give an idea of it, and we can only refer the student to more complete works on histology. An excellent book on the subject is "Guide to the Microscopic Examination of the Eye," by Prof. Greeff, of Berlin, translated from the 3rd

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German edition (1910) by Dr. Hugh Walker, of Glasgow, and published by the Ophthalmoscope Press, Ltd. (now the *British Journal of Ophthalmology*), Thayer Street, Manchester Square, London, W. The book is replete with useful practical information and constitutes a most valuable *vade mecum* for the microscopist.

**A Convenient Form of Microscopic Stains.**

Though we have given in the present part of this book a few hints for the preparation of the various staining media in general use, yet it will be undoubtedly more convenient for the student who wishes to do microscopic work to procure the stains ready made. They are obtainable in solution form in stoppered bottles from any firm of microscopic appliances makers, and also in the form of tablets or Soloids, from Messrs. Burroughs, Wellcome & Co., Ltd. The latter form is particularly well adapted to the requirements of the amateur microscopist, the various media being supplied in tubes generally containing six tablets, each of which is dissolved according to the directions given in the label of the tube when the solution is required. The great advantage of this method is that the products keep indefinitely in solid form, while solutions are liable to become affected under ordinary atmospheric conditions.

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# APPENDIX.

## DESCRIPTION OF STEREOGRAMS.

As already stated, each Stereogram from No. I. to XIV. (both inclusive) is accompanied by a line drawing (figs. 38 to 51) serving as a key, and the lettering of which indicates the most important features when the plate is examined by means of a convenient form of stereoscope.[1]

**Stereogram I.** (fig. 38) shows the cavities and sinuses surrounding the orbit. The section is a vertical one, passing just posterior to the greater part of the superior and inferior orbital margins. The frontal sinus is well developed. The

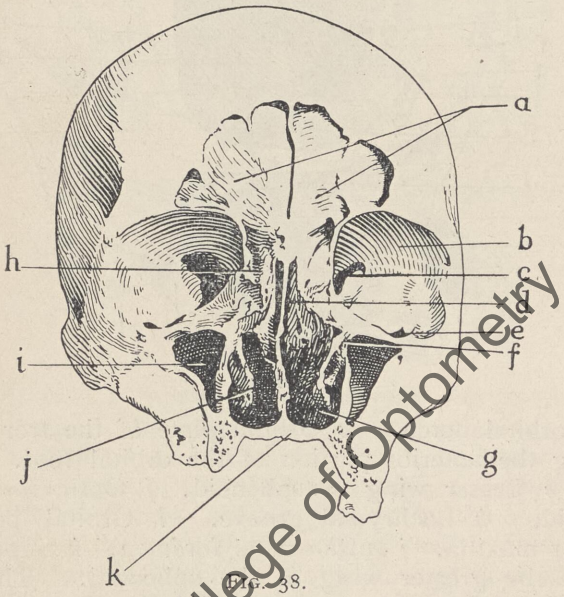


FIG. 38.

slope of the orbital floor, downwards to the temporal side, and, downwards anteriorly, shows clearly. *a* Frontal sinuses. *b* Orbital plate of frontal bone. *c* Sphenoidal fissure. *d* Nasal septum. *e* Anterior portion of spheno-maxillary fissure. *f* Lachrymal groove and canal. The canal, which opens into the inferior meatus of the nose, is occupied in

[1] Stereograms I and II are reproduced from Dr. Monthus's "Iconographie Stereoscopique Oculaire," by kind permission of the publishers, Messrs. Masson & Co., 120, Boulevard St. Germain, Paris.

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life, by the lachrymal sac. *h* Ethmoidal sinus. *i* Maxillary antrum (antrum of Highmore). *j* Inferior turbinate bone. *k* Palate bone.

**Stereogram II.** (fig. 39) permits the observation of the most important features of the orbital cavity. In this specimen the spheno-maxillary fissure widens, in two places, to an extent not frequently observed. *a* Frontal bone. *b*

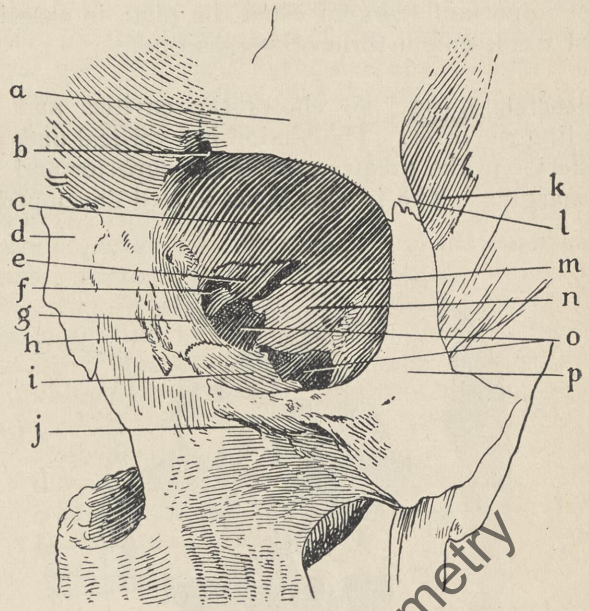


FIG. 39.

Supra-orbital notch. *c* Orbital plate of the frontal bone, forming the anterior portion of the orbital roof. *d* Nasal bone. *e* Lesser wing of sphenoid. *f* Optic foramen. *g* Ethmoid. *h* Lachrymal groove. *i* Orbital portion of superior maxilla. *j* Infra-orbital foramen. *k* Superior portion of the greater wing of the sphenoid. The orbital portion *n* of this bone is separated from the lesser wing of the sphenoid by the sphenoidal fissure *m*. *l* External angular process of the frontal bone. *o* Spheno-maxillary fissure. *p* Malar bone. In this stereogram the depth appears to be somewhat greater than its true value, this being due to an exaggeration of the stereoscopic effect.

**Stereogram III.** (fig. 40) represents an antero-posterior section through the globe of an adult, viewed slightly from the front.

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The iris is divided to one side of the contracted pupil; the remarkable flattening of the anterior lens surface is well shown. About 4 mms. to the left of the centre of the optic papilla a dark spot *m* indicates the position of the fovea centralis which is, in this specimen, on the surface of a swollen fold of the retina (the plica centralis) a post-mortem appearance which affects the retina especially in the region surrounding the macula lutea.

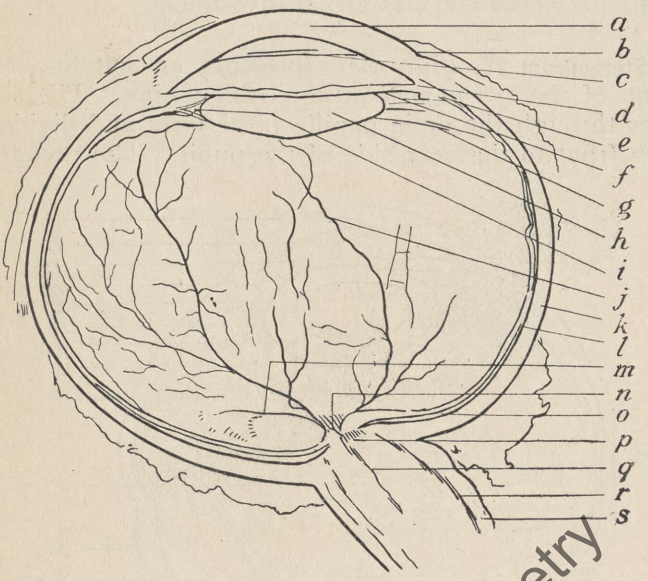


FIG. 40.

*a* Cornea. *b* Sulcus of the sclerotic corresponding to, and just behind, the outer sclero-corneal junction; *c* is the attached margin of the iris; this is seen to be finely irregular owing to the fibres of the pectinate ligament. Above it will be seen the faint linear shadow thrown by the sulcus circularis, which is not particularly well marked in this plate; *d* is the iridic angle, which is shown here as acute owing to the stretching of the iris whose pupil is contracted; the same letter *d* represents the point where the root of the iris, the ciliary muscle, and the fibres of the pectinate ligament are attached. *e* Ciliary processes; *f* the iris stretched straight across the aqueous chamber. Note that in this preparation the iris is cut to one side of a very contracted pupil. *g* Thickened edge of the physiological retina at the ora serrata; *h* is the crystalline lens, the anterior flat surface of which is in contact with the posterior surface of the iris: *i* is the location of the so-called canal of Petit between the fibres of

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the zonule of Zinn, the edge of the lens and the ciliary processes; *k* is the sclerotic; *l* is the optical or physiological part of the retina; *m* is the fovea centralis appearing on the surface of the plica centralis; *n* the optic papilla or optic nerve head with the physiological excavation at its centre; *o* the choroid; *p* the lamina cribrosa; *q* the central artery of the retina; *r* subarachnoidal space; *s* the dural sheath of the nerve, lined with the arachnoid membrane which surrounds the nerve and has a pial investment.

**Stereogram IV.** (fig. 41) represents an antero-posterior section of the eye of a man aged thirty-nine. The section passes through the optic papilla posteriorly and divides the iris in front to the near side of the pupil. The preparation

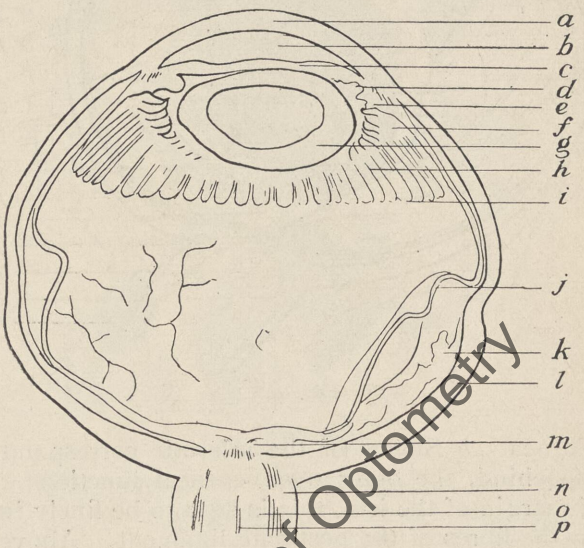


FIG. 41.

shows very well the ora serrata and the pars ciliaris retinæ. The retina has in places separated from the choroid, and the choroid is observed apart from the sclerotic. In this view the ligament of the lens is not seen. *a* Cornea. *b* Anterior chamber. *c* Iris, cut across to the near side of the pupil. *d* Posterior chamber. *e* Ciliary body. *f* Ciliary processes. *g* Lens crystallina. *h* Pars ciliaris retinæ, orbiculus ciliaris displaying a striated appearance. *i* Ora serrata—the edge of the pars optica retinæ. *j* The retina detached from the choroid. *k* Choroid, detached from the sclera, here displays the fibres of the lamina fusca. *l* Sclerotic. *m* Optic papilla

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with the optic cup in its centre. *n* Dura-matral sheath of optic nerve. *o* Optic nerve. *p* Arteria centralis retinæ.

**Stereogram V.** (fig. 42). Antero-posterior section through the eye of a man of 39. Same specimen as that shown in previous stereogram. The lens with its capsule and the vitreous have been removed; immediately in front

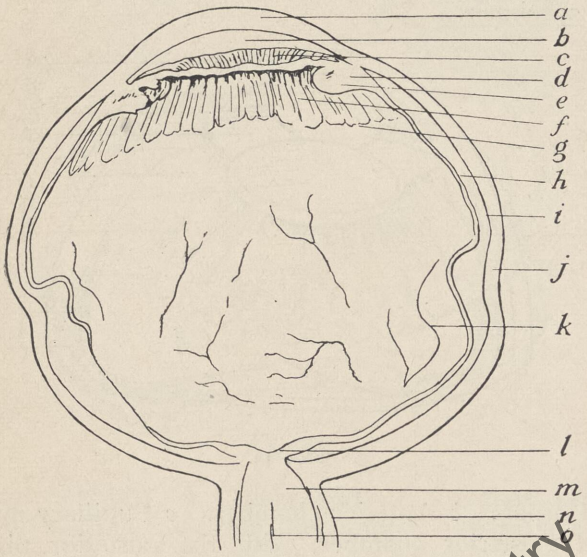


FIG. 42.

of the attached margin of the iris the shadow cast by the sulcus circularis corneæ can be seen. The ciliary processes are well displayed and the orbiculus ciliaris is well shown. The retina is in great part detached, but along the line of the ora serrata it is seen to be more firmly fixed to the subjacent structures; posteriorly the optic cup is clearly shown.

*a* Cornea. *b* Anterior chamber. *c* Iris; immediately in front of its attached circumference evidence of the sulcus circularis corneæ may be seen. *d* Ciliary body. *e* Ciliary processes. *f* Orbiculus ciliaris with meridional fibres. *g* Ora serrata. *h* Retina. *i* Choroid. *j* Sclerotic. *k* Retinal vessels. *l* Optic papilla and optic cup. *m* Optic nerve. *n* Dura-matral sheath of optic nerve. *o* Arteria centralis retinæ.

**Stereogram VI.** (fig. 43). Anterior half of an antero-posterior section of the eye viewed obliquely from behind.

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The ora serrata is well seen; along this goffered edge the retina is seen to be more firmly attached to the subjacent choroid than it is posteriorly. The radial arrangement of the orbiculus ciliaris is clearly shown on the left of the specimen. The pigmented posterior surface of the iris is displayed, forming the anterior wall of the posterior chamber. In this photograph the light has failed to catch the fibres of the ligament of the lens, so that they are not revealed in the specimen.

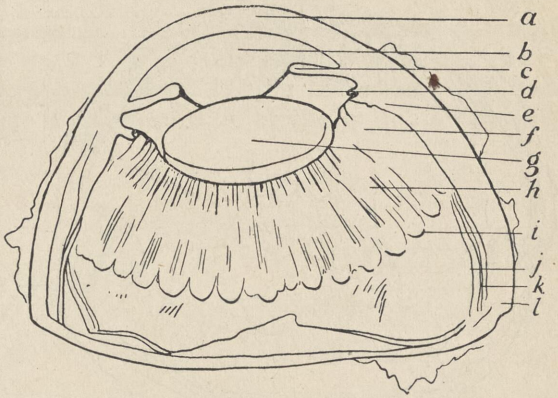


FIG. 43.

*a* Cornea. *b* Anterior chamber. *c* Pupillary margin of iris. *d* Posterior chamber, with the posterior pigmented surface of the iris in front, and the blunt anterior extremities of the ciliary processes projecting into it posteriorly; the zonule of Zinn is not here seen. *e* Ciliary body. *f* Ciliary processes. *g* Lens. *h* Orbiculus ciliaris, overlain by the pars ciliaris retinæ. *i* Ora serrata. *j* Retina. *k* Choroid. *l* Sclerotic.

**Stereogram VII.** (fig. 44). Antero-posterior section through the fore part of the globe of the eye. This section shows very well the suspensory ligament of the lens, particularly on the left side. As will be seen, the fibres of the zonule of Zinn spring from the ciliary body and the orbiculus ciliaris; they separate as they pass to the lens, some going to the front, others to the posterior surface of that structure; between the diverging fibres and the circumference of the lens is a space shown in section, *g*, the canal of Petit. The section also displays the relationship of the sulcus scleræ (*c*), at the junction externally of the cornea and sclerotic, to the sulcus circularis corneæ (*e*) situated at the angulus iridis.

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*a* Cornea. *b* Anterior chamber. *c* Sulcus scleræ. *d* Iris. *e* Sulcus circularis corneæ. *f* Posterior chamber bounded behind by the ciliary processes and the ligament of the lens. *g* The canal of Petit with the zonular fibres in

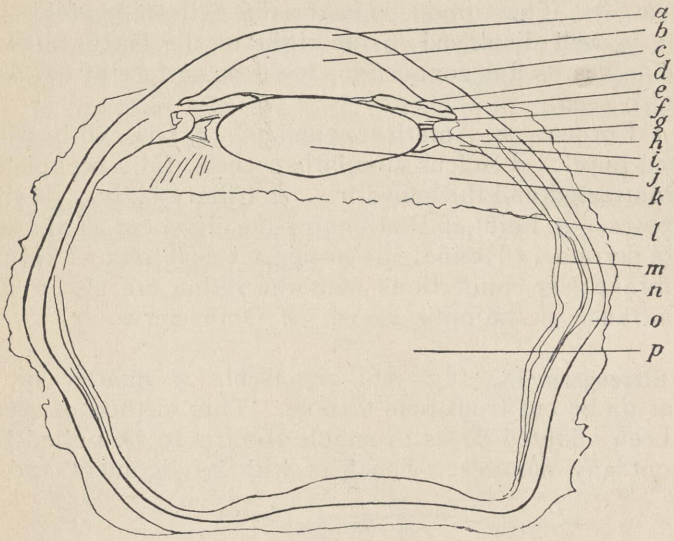


FIG. 44.

front and behind. *h* Ciliary body. *i* Ciliary processes. *j* Lens crystallina. *k* Orbiculus ciliaris. *l* Ora serrata. *m* Retina. *n* Choroid. *o* Sclera. *p* Corpus vitreum.

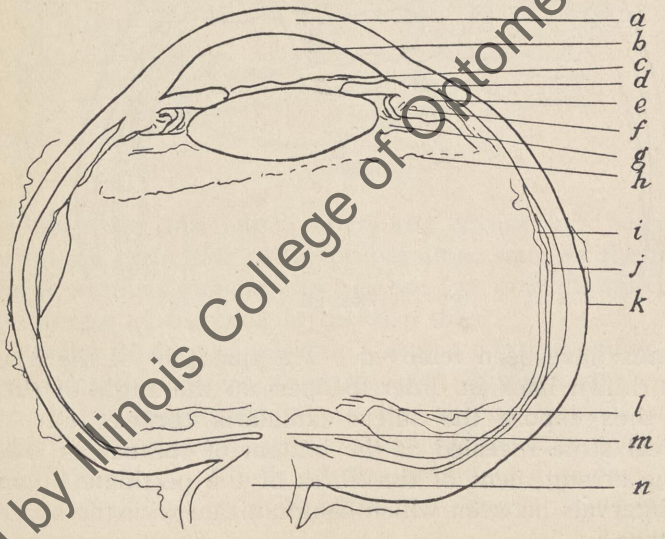


FIG. 45.

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**Stereogram VIII.** (fig. 45). Antero-posterior section through the eye. The pupil is widely dilated, with consequent thickening of the iris, which at its circumference is now seen to occupy almost completely the sulcus circularis corneæ (*d*). The vitreous is *in situ*; its delicate hyaloid membrane is well displayed to the right of the entrance of the optic nerve; its fine connections with the surface of the retina are also seen.

*a* Cornea. *b* Anterior chamber. *c* Iris, with widely dilated pupil. *d* Sulcus circularis corneæ, fully occupied by the contracted and thickened iris. *e* Ciliary body. *f* Ciliary processes. *g* Faint indications of the ligament of the lens. *h* Ora serrata. *i* Retina. *j* Choroid. *k* Sclerotic. *l* Hyaloid membrane; its connections with the retina are also visible. *m* Entrance of the optic nerve. *n* Optic nerve.

**Stereogram IX.** (fig. 46) represents a quarter of the ocular globe cut from pole to pole. This method of section has been adopted so as to enable the iris to be pulled back without any damage. The lens with its ligament and the

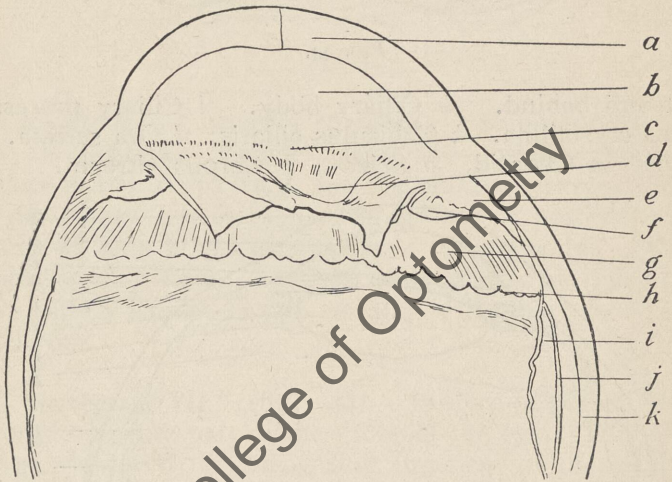


FIG. 46.

vitreous have been removed. The quadrant of the iris has been drawn back in order to open up the angle of the iris and thus expose the sulcus circularis corneæ (*c*). The vertical striæ revealed at the bottom of the sulcus are due to the arrangement of the fibres of the pectinate ligament, the intervals between which communicate with the spaces of Fontana.

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*a* Cornea. *b* Anterior chamber. *c* Sulcus circularis corneæ, at the bottom of which the vertically disposed fibres of the pectinate ligament can be faintly seen. *d* The iris pulled back. *e* Ciliary body. *f* Ciliary processes. *e* Orbiculus ciliaris. *h* Ora serrata; here the œdema of the pars optica retinæ, due either to post-mortem changes or the influence of the preservative, is very definitely limited in front in harmony with the attached edge of the ora serrata. *i* Retina. *j* Choroid. *k* Sclerotic.

**Stereogram X.** (fig. 47). View of the anterior surface of the eyeball, the cornea having been cut away and the anterior chamber laid open.

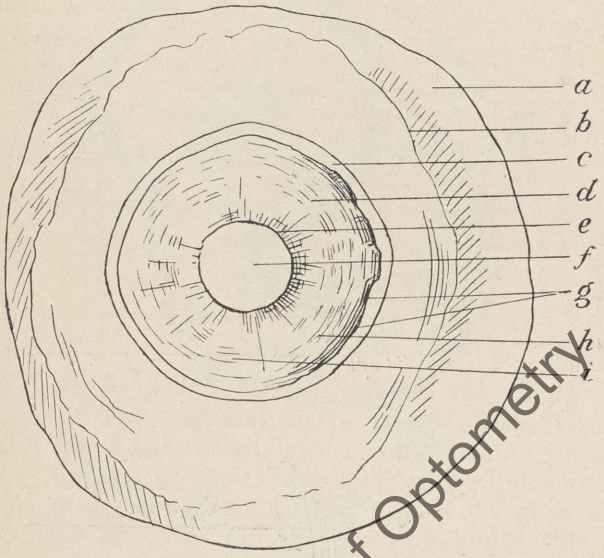


FIG. 47.

Under the thin edge, where the cornea has been cut away on the right side of the preparation, some of the fibres of the pectinate ligament can be seen (*g*) with the openings of the spaces of Fontana in between them.

*a* Outer surface of sclerotic. *b* Cut edge of ocular conjunctiva. *c* Sclero-corneal margin cut through and cornea removed. *d* Anterior chamber, with anterior surface of iris behind. *e* Pupillary margin of iris. *f* Crystalline lens, seen through pupil. *g* Fibres of the pectinate ligament with openings of the spaces of Fontana. *h* Circular folds of iris. *i* Radial folds of iris.

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**Stereogram XI.** (fig. 48). Anterior view of the eye, the cornea and sclerotic having been removed.

The iridic angle is thus exposed from the front (*c*) and the fibres passing from the cornea to the front of the iris, which constitute the pectinate ligament, are well displayed; in the intervals between these fibres there are openings leading into the crypt-like spaces—the spaces of Fontana. Just external to the ciliary margin of the iris (*c*) may be seen a narrow annular band surrounding the iris; this marks the anterior attachment of the meridional fibres of the ciliary muscle to the internal scleral process.

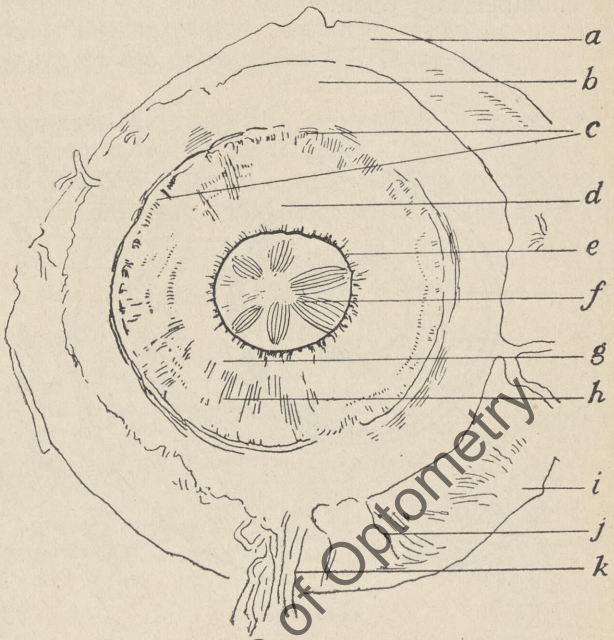


FIG. 48.

*a* Choroid. *b* Scleral surface of the ciliary body. *c* marks the position of the spaces of Fontana, the openings of which appear between the fibres of the pectinate ligament. Just external to *c* may be seen the line of attachment of the anterior ends of the meridional fibres of the ciliary muscle. *d* Convexity of the iris overlying the sphincter pupillæ. *e* The pupillary margin of the iris. *f* Lens seen through pupil. *g* Circular folds of the iris. *h* Radial folds of the iris. *i* Venæ vorticosæ of the choroid. *j* Long posterior ciliary artery. *k* Ciliary nerve.

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**Stereogram XII** (fig. 49). View of the anterior surface of the eye, the sclerotic and the cornea having been removed. The right half of the iris has been cut away so as to open the posterior chamber, the posterior wall of which is thus exposed; this is seen to be formed, from without inwards, by the blunt anterior extremities of the ciliary processes (*e*), the zonule of Zinn composed of the fibres which form the ligament of the lens (*d*), and the anterior

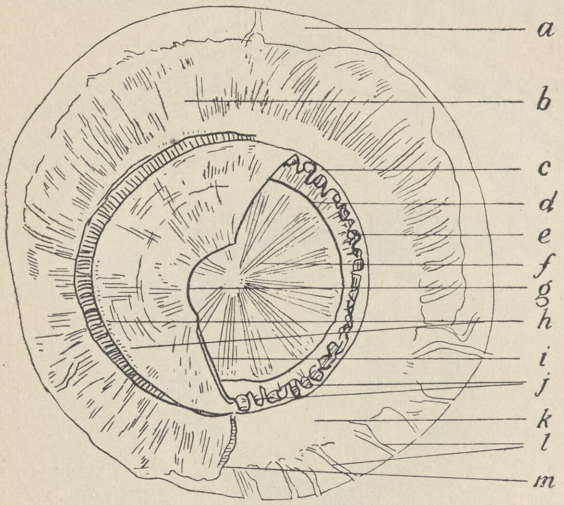


FIG. 49.

surface of the lens (*f*). The cut edge of the ciliary margin of the iris (*c*) is shown, and certain narrow folds (*j*) are seen divided. These are the radially arranged folds which pass from the forepart of the ciliary body and ciliary processes on to the posterior surface of the iris, converging towards the pupillary margin. On the left and upper side of the preparation the outer layer of the ciliary body has been dissected away so as to expose the meridional fibres of the ciliary muscle and the vascular and nervous plexuses within its substance. Close to the ciliary margin of the iris on the left can be seen some of the fibres of the pectinate ligament and the openings of the spaces of Fontana.

*a* Choroid. *b* Meridional fibres of ciliary muscle, together with vessels and nerves. *c* Cut peripheral attachment of iris. *d* Zonule of Zinn, suspensory ligament of the lens. *e* Anterior extremities of the ciliary processes seen in shadow. *f* Lens. *g* Pupillary margin of iris. *h* Fibres of the pectinate ligament with the openings of the spaces of Fontana. *i* Cut edge of iris. *j* Folds passing from ciliary body and processes to posterior surface of iris (structural

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folds of Schwalbe). *k* Outer surface of ciliary body. *l* Ciliary nerves breaking up to form plexus. *m* Divided edge where superficial part of ciliary body has been removed.

**Stereogram XIII.** (fig. 50). View of the interior of the anterior half of the globe seen by reflected light. In the centre is seen the lens; around its circumference there is a narrow dark annular zone, the zonule of Zinn; here and there the striation produced by the fibres of the suspensory

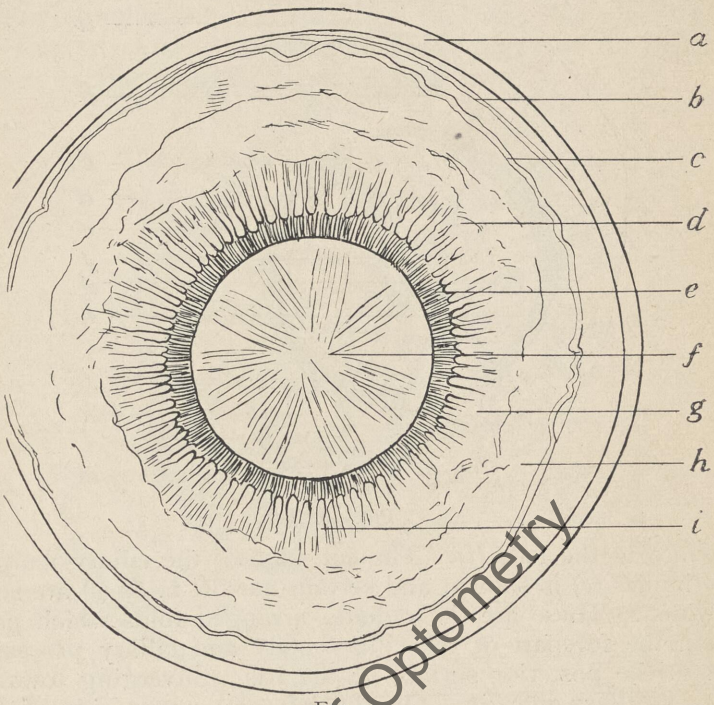


FIG. 50.

ligament can be faintly seen (*e*). External to the zonule, the corona ciliaris, formed by seventy or more ciliary processes, is well displayed (*d* and *g*). Wide of the elevations produced by the ciliary processes the orbiculus ciliaris is shown. The ora serrata of the retina is somewhat obscured by the puckering of the hyaloid membrane of the vitreous body.

*a* Sclerotic. *b* Choroid. *c* Retina. *d* Orbiculus ciliaris. *e* Zonule of Zinn; the fibres of the suspensory ligament of the lens can be faintly seen. *f* Posterior surface of the lens; along its circumference may be seen the points of attachment of some of the suspensory fibres. *g* The corona ciliaris. *h* The vitreous and puckered hyaloid membrane. *i* Ciliary processes.

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**Stereogram XIV.** (fig. 51). View of the interior of the anterior half of the globe of an adult. This photograph has been introduced because it shows very well the arrangement of the lamellæ of the lens, as seen from behind, to form the posterior lens star. As will be seen in this specimen, the tissue of the lens is disposed in eight wedge-shaped masses.

The lens also displays around its circumference a two-edged appearance. The vitreous and hyaloid membrane have been removed from the posterior surface of the lens,

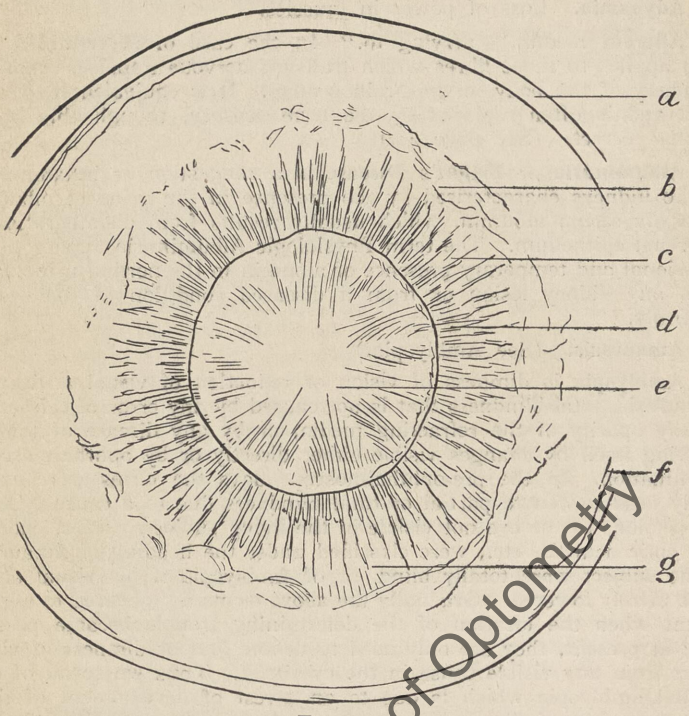


FIG. 51.

but the connection of the two seems to correspond to the edge of the circumference of the lens. To the anterior margin of the circumference may be seen passing the fibres of the suspensory ligament of the lens.

*a* Sclerotic. *b* Torn edge of the hyaloid membrane. *c* Corona ciliaris, formed of eighty-one ciliary processes. *d* Zonule of Zinn; the fibres of the suspensory ligament of the lens are here seen passing to the anterior aspect of the circumference of the lens. *e* Posterior surface of the lens, showing the lens star. *f* Retina. *g* Ridged and striated orbiculus ciliaris.



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# GLOSSARY.

**Acromegaly.** A curious disease in which together with ocular symptoms (Hemianopsia) there is an abnormal development of the extremities, especially the hands and feet. It is associated with a diseased condition of the pituitary body and of the thyroid gland.

**Acute.** Having a rapid onset, a short course and pronounced symptoms.

**Adynamia.** Loss of power in muscles.

**Afferent** means "carrying to." In the case of nerve fibres, the term applies to those fibres which transmit nervous impulses from the periphery of the body to the brain centres. It is equivalent to centripetal and is often replaced by the term sensory, though this is not strictly correct. (See page 42.)

**Albuminuria** or **Bright's Disease** is a congestion or inflammation of the kidneys characterised by the presence in the urine of albumin, generally serum albumin, which usually results from disintegration of the renal epithelium. The term Physiologic Albuminuria applies to the occasional and temporary presence of albumin in the normal urine apart from any kidney lesion or from a diseased condition of the system generally.

**Amaurosis.** (See Amblyopia.)

**Amblyopia** is dimness of vision or reduction of visual acuity and Amaurosis, total blindness that is not caused by any error of refraction, or any opacity of the refracting media, or by any disease of the eye showing itself by changes visible either directly or by ophthalmoscopic examination. In the pre-ophthalmoscope days the terms were extensively used to denote partial or total blindness due to a cause lying in the portions of the eye not visible in the living subject. Thus, choroiditis, optic neuritis, etc., were classified under the heading of Amaurosis if the subject were totally blind, or of Amblyopia if his visual acuity were merely lowered. Gradually the above terms disappeared to a great extent when the location of the determining trouble became possible and, at present, they are only used to denote loss or dimness of vision apart from any visible cause in the eye itself. Thus we speak of congenital amblyopia which is due to an arrest of development of some important part of the eye, most often the globe as a whole (microphthalmia) or the nervous apparatus of the eye; again, we observe cases of amblyopia ex-anopsia, i.e., amblyopia from disuse or from non-use of the eye as occurs in concomitant squint, the development of the defect being the effort of nature to prevent diplopia or double vision. In the same way we still speak of toxic amblyopia, though we know now that this condition is really retrobulbar neuritis (i.e., an inflammation of the optic nerve behind the globe) caused by various poisons, especially tobacco and alcohol. Similarly we have the type of amblyopia (and amaurosis) due to some disorder of the portion of the central nervous system which presides to vision. In fact, in the present state of ophthalmic science, amblyopia and amaurosis are respectively diminution or complete loss of visual acuity apart from any visible symptoms. As a wag puts it, in amblyopia the subject still sees a little and the ophthalmic surgeon does not see anything; in amaurosis, neither the subject nor the surgeon sees anything.

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**Amorphous** (from the Greek prefix *a*, meaning deprived of, and *morphe*, shape) a substance is amorphous when it is formless, shapeless, and of uniform homogeneous structure, like a mass of glass, by contra-distinction with crystalline substances the molecules of which are arranged in a definite geometric order.

**Analysis.** A chemical term denoting the resolution of a compound body into its constituent elements. For instance, if an electric current is made to pass into water (rendered more conductive by the addition of a few drops of sulphuric acid) it is found that two volumes of hydrogen are liberated at the negative pole or cathode and one volume of oxygen at the positive pole or anode. This operation constitutes the electrolytic analysis of water.

**Anastomosis.** This term generally means intercommunication of two or more blood-vessels more or less remote from each other.

**Anthropology.** The Greek prefix *anthropo*, means " relating to man or to the human race." Anthropology is the branch of science concerned with the study of the human race.

**Aphakia.** The condition of an eye deprived of the crystalline lens.

**Aphasia.** Partial or complete loss of the power of expressing ideas by means of speech or writing. Aphasia may be either motor or sensory.

Motor aphasia consists in loss of the power of speech owing to inability to perform the various movements of the mouth and larynx necessary for the articulation of words. The muscles concerned in these movements are not co-ordinated owing to disease of the cortical centre for speech.

Motor aphasia is usually accompanied by agraphia, i.e., inability to write, and by right hemiplegia. The cortical centres for articulate language are supposed to be divided into four subcentres, namely, a visual centre for words, an auditory centre for words, a motor centre for articulate speech, and a motor centre for written language. Lesions of one or more of these subcentres produce the characteristic forms of motor aphasia.

Sensory aphasia or Amnesia is the loss of memory for words and may exist alone or in conjunction with motor aphasia. It occurs in three main forms: (1) simple loss of memory for words; (2) word-deafness or inability to understand spoken words; and (3) word-blindness or inability to understand written or printed words.

**Aponeurosis** (plural aponeuroses) denotes a fibrous, membranous expansion of a tendon giving attachment to muscles or serving to enclose and bind down muscles.

**Apoplexy.** The condition resulting from hemorrhage or from the plugging of a blood-vessel especially in the brain or the spinal cord. The word apoplexy is sometimes also applied to the bursting of a vessel in other parts, e.g., the lungs, or the retina. In such cases, however, the term hemorrhage is more frequently used.

**Arborisation.** (See Neuron.)

**Artefact.** A structure that has been produced by mechanical, or chemical, or other artificial means, or a structure or tissue that has been changed from its natural state by artificial means. The term is often used in microscopical and histological work to denote structures which are due to the mechanical or chemical effects of the media used for hardening, fixing, etc.

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**Arthropoda.** The class of invertebrate creatures with jointed limbs like crabs and spiders. See Classification of Living Beings. The term Articulata is often used as synonymous to Arthropoda.

**Articulation** or **joint** denotes the union of two contiguous bones together with the parts forming the connection. There are in the body movable joints and fixed joints. That uniting the upper end of the thigh bone or femur to the bone of the pelvis represents a typical movable joint of the ball-and-socket kind. In joints of this kind the bony surfaces which move upon each other are covered with cartilage and between them is placed a sort of sac which lines the cartilage and to a certain extent forms the sidewalls of the joint. This sac, somewhat similar to a serous membrane, secretes a small quantity of viscid, lubricating fluid termed the synovia. The bones of the skull are joined together by a kind of dovetailed arrangement of their edges, which represents the type of fixed joints.

Between the two kinds of articulation, namely, the movable and the fixed joints, there are examples of imperfect joints in which the conjoined bones present no smooth surfaces capable of rotatory motion but are connected by continuous cartilages or ligaments and have only so much motility as is permitted by the flexibility of the joining substance. Examples of such joints are found in the vertebral column, the flat surfaces of the bodies of the vertebræ being connected by thick plates of flexible fibro-cartilage which confer upon the whole a fair amount of play and springiness and yet prevent any great extent of motion between the several vertebræ.

**Ascending** with respect to the central nervous system means afferent or headwards.

**Astringent.** Checking hemorrhage by contracting the blood-vessels. The term Styptic (which is derived from the Greek word meaning astringent) is frequently used in the same sense.

**Atavism.** The appearance of a peculiarity in an individual whose more or less remote ancestors possessed the same peculiarity but whose immediate ancestors did not present it.

**Ataxia.** Lack of co-ordination of muscular movements such as occurs in diseases of the cerebellum, or in sclerosis of the posterior columns of the spinal cord as is the case in locomotor ataxia or tabes dorsalis.

**Atonia.** Loss of tone in muscles.

**Atrophy.** Diminution in the size of a tissue or an organ or a part of the body, the result of degeneration of the cells or decrease in the size of the cells.

**Autolysis** (or Autodigestion). Digestion of an organ by its own secretion. The term also applies to the self digestion of inflammatory exudates and necrotic material in the living body.

**Axis-cylinder** or **Neuraxon** of a nerve fibre is the central living core which transmits or conducts nerve impulses.

**Bacterium** (plural bacteria). The word was at first applied to microscopic unicellular living beings, of a rod-like shape, belonging to the lowest ranks of the living world. The term is now used indiscriminately for the whole group of such organisms, irrespective of their form, the term bacillus being reserved for those which resemble a rod in shape. About fifty years ago, when scientists first turned their attention to this field of research, a somewhat heated discussion arose between botanists and zoologists as to whether bacteria belonged to the

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vegetable or the animal kingdom. The dispute seems to be settled in favour of the claims of the former, but a truce has been arrived at through the efforts of Sedillot (a French microscopist) who, in 1878, suggested the term microbe (from the Greek words *micros* small, and *bios* life), the use of which does not imply a decision in favour of either party. At present the word microbe is still useful to describe microscopic organisms, both vegetable and animal, or where doubts yet exist as to which of the two groups should contain them.

A similar use is made of the term Germ which merely signifies some rudimentary form of living matter whether plant or animal. Indeed, the dispute mentioned above is somewhat profitless, as the terms plants and animals were of course used long before these simpler and intermediate forms of life were discovered. It is obviously easy to distinguish a cat from a cabbage, or a butterfly from a flower, but as we pass lower and lower down the scale it becomes more and more difficult and, in truth, at the very bottom, no hard and fast line of demarcation can be drawn between the two categories.

Bacteriologists are still in doubt as to whether some of the organisms they deal with should be classified as animals or plants. Their difficulty is further increased by the comparatively recent discovery of still smaller living organisms, the so-called ultra-microscopic or filter passers. These organisms are so minute that they are scarcely visible or even quite invisible with the highest power at present available, but their presence can be detected by the ultra-microscope; hence the name of ultra-microscopic applied to them (see ultra-microscope); the other name (filter passers) is derived from the fact that owing to their small size these organisms can pass through the various filters which retain the larger forms. It has been ascertained experimentally that the organisms in question are the cause of certain diseases such as smallpox, yellow fever, and other acute infective fevers, including, in all probability, measles, scarlet fever, etc. Thus, at the lowest rung of the ladder of life, there are numerous very simple forms, the animal gradually merging with the vegetable and to denote this group of simplest form, Haeckel has proposed the term Protists, which include both the most primitive plants and the most primitive animals or Protozoa. Further details on the subject of Bacteria generally are given in Chapter VI.

**Biology** is the branch of science concerned with the structure, the function and the organisation of living beings generally.

**Bright's Disease** (or **Nephritis**). See Albuminuria. The term nephritis means inflammation of the kidneys.

**Bulb** (spinal) or **Medulla oblongata**. That portion of the central nervous system extending from the spinal cord to the cerebrum and containing some of the most important vital centres of the body.

**Cartilage** or **Gristle** is a white semi-opaque non-vascular connective tissue composed of a matrix containing nucleated cells which lie in spaces or lacunæ of the matrix. As do all forms of connective tissues cartilage yields, when boiled in water, a substance called chondrin which is chemically akin to gelatine. Bones in the embryo, and in the young, are made of cartilage which is gradually transformed into true bone (see Ossification).

Cartilage occurs in the adult to join the ribs together (costal cartilage), to invest the ends of bones at the joints; it enters into the structure of the pharynx, the larynx, the trachea or wind-pipe. It also serves to connect and bind the intervertebral discs of the vertebral column. Generally speaking, it assists in binding bones together yet

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allowing a certain degree of movement; it acts as a buffer to deaden shocks, it reduces friction at joints, and serves to keep open and maintain the shape of tubes, as in the trachea; it forms attachments for some muscles and ligaments. The costal or rib cartilages form an important part of the framework of the thorax and impart to its walls the elasticity which is necessary to the performance of respiratory movements.

**Catarrh** is inflammation of a mucous membrane.

**Catoptric** is the branch of optics concerned with the reflection of light at polished surfaces. A catoptric image is an image formed by reflection at a surface acting as a mirror. Thus we speak of the catoptric corneal images, or of the catoptric lenticular images which are due to reflection at the corneal and lenticular surfaces respectively. The portion of incident light serving to form the corneal and lenticular catoptric images is lost so far as vision is concerned, but these images are made use of to ascertain the shape and curvature of the surfaces which give rise to them.

**Cellulifugal** applies to impulses proceeding from a nervous cell in the central nervous system and propagated along the axon of the cell towards a peripheral organ. With respect to the cell considered the term cellulifugal is equivalent to efferent.

**Cellulipetal** applies to an impulse brought to a nervous cell (via its dendritic processes) from some other nervous cell. Equivalent to afferent.

**Centres (Nerve).** Nerve-cells or groups of nerve-cells devoted to the performance of some definite physiological function. Sensory centres in the cerebral cortex are the physical bases of sensations. Motor or Psychomotor centres in the cortex send down impulses to determine the contraction of certain groups of muscles and also to maintain the tone of muscles generally.

**Centrifugal.** (See Efferent.)

**Centripetal.** (See Afferent.)

**Cerebellum** literally means small brain. It is a mass of grey nervous matter sending fibres to the cerebrum and receiving fibres from the body, especially the muscles, via the spinal cord. Its activities do not rouse consciousness and it is mainly concerned with the balancing and equilibrium of the body and the co-ordination of the muscular action generally.

**Cerebrum.** Strictly speaking the term applies to the portion of the cerebro-spinal system that is lodged in the skull cavity, but very often it is understood to mean the brain proper, i.e., the cerebral hemispheres with their outer convoluted surface of grey matter (the cerebral cortex), together with the various masses of grey matter (or basal centres) forming the greater part of the mid- and end-brain and the association bundles of fibres (white matter) connecting the cortex and the basal centres. The cerebral cortex governs voluntary movements and is the physical basis of consciousness, will and intellectual functions. The basal centres are mostly concerned with the regulation and control of the numerous phenomena, the collection of which constitute the physiological and nutritional activities of the individual. The cerebellum, though located in the skull cavity, is not usually regarded as forming part of the cerebrum (see cerebellum).

**Chronic**, of long duration. Opposite to acute.

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**Classification of Living Beings.** Naturalists have for a long time divided all the substances and organisms existing in the universe into three main groups, the mineral world, the vegetal world, and the animal world. According to Linneus, the characteristics of these three main groups may be summarised as follows:—*Mineralia sunt* (i.e., minerals exist), and apart from atmospheric and other chemical actions, they do not die in the usual sense of the term. *Vegetalia sunt et crescunt* (i.e., exist and grow), and, ultimately die. *Animalia sunt, crescunt et sentiunt* (i.e., exist, grow, feel), and, ultimately die.

These characteristics must not be taken too literally. It is a well known fact that a crystal of mineral substance, e.g., a crystal of common salt or a crystal of sulphate of copper, immersed in an aqueous solution of ordinary salt or of copper sulphate, gradually increases in size by adjunction of solid molecules derived from the solution, which arrange themselves on the surfaces of the original crystal in a regular and geometric order. This growth of a mineral crystal cannot, however, be compared to the growth of a plant or of an animal. Again, sensibility, i.e., the power of responding to external stimuli, which, according to Linneus forms the main difference between the animal and the vegetal world, is not an absolute criterion. Many plants manifest an aptitude to react under the influence of external stimulation and have, therefore, a certain degree of sensibility. Beside the phenomena of Heliotropism mentioned in Chapter VII., it is a well-known fact that the leaves of the mimosa fold themselves on the merest contact of an external object.

Other naturalists thought they had found a distinctive character between animals and plants in the existence of a digestive apparatus in the former while the latter are deprived of such organs. It has been ascertained, however, that certain plants, termed carnivorous or insectivorous, have organs which permit them to seize insects and small animals and to digest the animal substance, which is thus assimilated very much as is the case in carnivorous or insectivorous animals.

It is, however, in the matter of the relation of animals and plants with the atmosphere that an antagonism has been thought to exist between the living conditions of animals and plants. Lavoisier was the first to find out that a living animal absorbs oxygen from the atmosphere and rejects carbonic acid gas, while a green plant under the influence of the sun absorbs carbonic acid gas from the atmosphere and rejects oxygen. Besides, the living animal spends and transforms into heat or movement or electricity the chemical energy stored up in its food and produces as a result water in the form of steam, carbonic acid gas, and other waste products containing nitrogen, like urea. The living plant, on the other hand, receives calorific and luminous energy from the solar radiation and by means of its green parts stores that energy by production of materials such as starch, sugar, etc.

In fact, the chemical actions which take place in plants under the influence of light constitute some of the most important phenomena in the economy of our terrestrial world; without such actions, life would become impossible. We know that living animals constantly absorb the oxygen of the atmosphere and reject carbonic acid gas and water; in the dark, plants respire in the same way, absorbing oxygen and exhaling carbonic acid and water. It would seem, therefore, that our atmosphere must gradually lose all its oxygen and become richer in carbonic acid gas. That it is not so, and that the composition of air remains remarkably constant, are well known facts; this is due to the green colouring matter of plants, the chlorophyll, acting in an opposite direction.

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Under the influence of light, the chlorophyll decomposes the carbonic acid gas and water of the atmosphere, fixing the carbon and hydrogen in the tissues of the plant in the form of glucose, starch, and similar bodies, and rejecting the oxygen. This function, termed the chlorophyllian function, can only occur in the presence of light; it is light which is capable of determining the chlorophyll of the plants to abandon its physiological inertia, and to perform the part assigned to it in vegetal life.

We find this chlorophyllian function in the lower groups of the animal series, especially in Infusoria, where it presents the same character as in the vegetal world; but in the animal kingdom the action of light assumes the most varied forms, as we have seen in Chapter VII.

For the convenience of the reader who is not familiar with zoology we give below a brief account of the classification of animal living beings.

Animals may be classified into Vertebrates (Vertebrata) and Invertebrates (Invertebrata). The name Vertebrate, which means "jointed," refers to the possession of a jointed bony internal axis as the main part of the skeleton. This jointed axis is the vertebral column or backbone. In the lower forms of vertebrata this axis is not so well developed and, in the place of it, there is a smooth, elastic cartilaginous rod which has been termed the notochord (or back string). In all true vertebrate animals, the notochord is present at some stage of development, although in the higher forms it subsequently becomes surrounded and nearly obliterated by the jointed bony rod or vertebral column.

Vertebrate animals are divided into: (a) Ascidians which form the transition between Vertebrates and Invertebrates, a typical example of which is the Amphyoxus or Lancelet, a kind of worm-like creature living at the bottom of the sea and generally burrowing its way in the sand. It reaches a length of 7 or 8 mms. and has a very simple form of skeleton reduced to the notochord which we find in the embryo of all vertebrate animals; (b) Fishes; (c) Amphibians; (d) Reptiles; (e) Birds; and (f) Mammals.

Invertebrate animals are those in which neither notochord nor vertebral column is present. They are classified into: (a) Arthropodes (Arthropoda), (b) Worms (Annelida), (c) Molluscs, (d) Echinodermes (Echinodermata), (e) Cœlenterates (Cœlenterata), (f) Protists (Protozoa).

Arthropodes, which include Insects, Crustaceans, Spiders and Myriapodes, have three characters in common. (1) The body is formed of segments placed one after the other, most of these segments carrying a pair of articulated limbs serving to locomotion. Those limbs attached to the anterior segments in the neighbourhood of the mouth, are especially adapted to the prehension and the mastication of food. (2) The body is covered externally by a thick layer of hard substance (chitine) which, however, remains thinner and flexible at the lines of junction of the various segments, in order to permit free movement of the body. This chitinous layer derives from the simple epidermic layer which covers the body of the young and gradually thickens and hardens by multiplication of its cells. The outermost surface of the chitinous envelope is frequently impregnated by calcareous matter which increases its resisting power; such is the case in the crayfish. (3) The rigidity of the chitinous envelope would necessarily prevent the growth of the animal, and it is for this reason that, during the period of development, the external and harder part of the envelope is periodically shed off, the envelope being then reduced to its soft and flexible internal layer;

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it is during this period of softening that the growth of the animal takes place. Then, the original envelope is formed again by multiplication and hardening of the cells of the internal layers and the growth remains stationary till the next period of shedding occurs.

The class of Arthropodes includes Insects, Crustaceans, Spiders and Myriapodes.

In insects, the body is made of a number of segments in which three parts are very distinctly seen, namely, the head, the thorax and the abdomen. The head made of a single piece, carries the mouth, the eyes and five pairs of articulated limbs; the first pair, on the front, constitutes the antennæ or feelers, which serve as organs of tactile sensibility and as olfactory organs; the other four pairs surround the mouth and serve to the prehension and the mastication of food. The thorax consists of three segments, each of which has a pair of articulated legs on the lower surface, while the two posterior ones have, in addition, a pair of wings each on their upper surface. The abdomen is made of a variable number of segments (from eleven to five) strongly attached to each other. It does not carry any limb but is perforated on either side by openings through which air is supplied to the respiratory organ. In some species (wasp, bee) the end part of the abdomen is fitted with a process or sting by means of which the insect may instil the poison elaborated in some special form of racemose glands.

The Crustaceans are characterised by an immovable junction of the head and thorax which thus form a single piece, the cephalo-thorax, usually covered by a strong chitinous or calcareous envelope also made of a single piece. The abdomen is made of a number of segments like those of insects. Beside the antennæ the cephalo-thorax is fitted with a number of articulated legs; there are five pairs in the lobster and the crayfish, the front pair being much more developed than the others.

In spiders the body is made of a cephalo-thorax and an abdomen generally separated by a narrowing. Four pairs of legs are fitted to the cephalo-thorax. The front part of the head carries two pairs of articulated processes, one pair serving to the prehension and mastication of food, the other giving passage to the poison secreted by poison glands which serve to the animal to kill its prey.

The Myriapodes (or Centipedes or Millipedes) have an elongated body, the anterior part of which, the head, is followed by a great number of segments, each of which carries a pair of articulated legs and all of which are similar to each other, so that there is no possible distinction between the thorax and the abdomen as is the case in other Arthropodes. The head carries, like that of insects, five pairs of articulated limbs, one of which (the antennæ) serves as an organ of tactile sensibility, the other four pairs around the mouth constituting organs for the prehension and mastication of food.

The class of Worms (Annelida) includes an immense variety of forms, the common character of which is that the body is made of a number of segments joined to each other (as can be seen in the leech and the earthworm) these segments do not carry any articulated limbs and the body generally is covered by a soft envelope without trace of chitinous or calcareous formation. The general arrangement of the various organs serving to digestion, respiration, circulation, etc., presents wide differences according to the conditions of life of the animal considered. Some are aquatic, some others live in the ground (earthworm) and numerous species live in a parasitic state in the body of some other animal (e.g., the tapeworm). The molluscs are invertebrate animals in which no segmentation is apparent, as is the case in

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arthropodes, and whose body is protected by a calcareous shell made of a single piece (snail) or of two pieces or valves (oyster). Molluscs are sub-divided into: (a) Cephalopodes (cuttle fish; octopus) in which a variable number of fleshy processes or tentacles fitted with suckers surround the head. (b) Gasteropodes (snail) in which the shell is made of a single piece, more or less convoluted and the lower part of the body is produced into a roughly triangular muscular outgrowth called the foot on which the animal crawls. The dome-like dorsal part of the body containing the chief viscera is well protected by the shell. The walls on either side of the body are produced into free folds, the pair of which makes up the mantle.

(c) Lamellibranches, represented by the mussel and the oyster, are also called acephale because they have no distinct head, or bi-valves, as their shell is made of two halves or valves the animal can open or close at will.

The Echinodermes, including the starfish and the sea-urchins are all living in sea water. Their body is protected by plates of calcareous matter and by hard pricking processes.

The Cœlenterates, represented by the hydra, the medusa, the sea anemone, the jelly fish, etc., constitute the lowest class of living beings whose body is made of a collection of cells. This body consists of a sac with a single opening to enable nutriment to enter it. They are mostly sea animals and are usually fixed to rocks, some, like the sea anemone, living singly, while others, like corals, form colonies. The class of Protists (Protozoa) are on the borderland between the animal and the vegetal world. They are reduced to a single cell and are represented by the amœba we have described in Chapter II. Fuller particulars on the subject of Protozoa will be found under the headings of Bacterium and Ultra-microscope.

It must be understood that this classification has no pretention to be complete, and is merely intended as a rough guide to the relative position of living beings in the zoological scale.

**Commissure** (from the Latin *com*, together, and *mittere*, to send). Anything which unites two parts. We have alluded to the grey and the white commissures of the spinal cord and also to the corpus callosum, a bundle of fibres forming a bridge which connects the two cerebral hemispheres.

**Congenital.** A condition existing at birth.

**Consciousness.** Personal experience or awareness of one's body and of the surrounding world mainly resulting from perception and sensations. Consciousness might be defined as the totality of mental occurrences such as thoughts, emotions and memories.

**Cord (Spinal).** The lowest or hind part of the cerebro-spinal system which is lodged in the central canal of the vertebral column and is connected anteriorly with the brain proper or cerebrum by the bulb or medulla oblongata. The cord receives nerves from all parts of the body, sends out nerves to all parts and possesses in its grey matter a number of nerve centres.

**Corium.** The deep layer of the skin and of the mucous membranes.

**Corticifugal.** The suffix " fugal " means away from. The term corticifugal applies to a nervous impulse transmitted from the cerebral cortex towards some peripheral part or organ. It is, in fact, equivalent to centrifugal or efferent.

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**Coryza** is catarrh of the mucous membrane of the nasal air passages and adjacent sinuses or air cells, popularly called "cold in the head."

**Crepuscular Vision.** See Diurnal Vision.

**Decussation.** This term denotes an x-shaped crossing, especially of symmetrical parts, as nerve fibres or nerve tracts. The principal decussations we are concerned with are (a) the complete decussation of the lateral pyramidal tracts of the spinal cord which cross in the bulb, from which they are distributed to the cerebral hemispheres. It follows that a lesion in one of the hemispheres of the brain will cause paralysis of the limbs on the opposite side of the body; (b) the optic chiasma or partial crossing of the fibres of the two optic nerves. Beyond the chiasma the optic nerve fibres form the optic tracts, each of which contains fibres proceeding from the eye on the same side and fibres proceeding from the eye on the other side.

**Diabetis.** A nutritional disease characterised by the habitual discharge of an excessive quantity of urine containing sugar; there is usually intense thirst, with voracious appetite, progressive loss of flesh and strength and a tendency to fatal termination.

**Diapedesis.** The passage of the blood through the unruptured blood-vessel walls.

**Diurnal Vision** is the kind of vision taking place in ordinary daylight or in artificial light having the average intensity of ordinary daylight. The term is used by contradistinction with nocturnal or more exactly crepuscular vision which occurs in animals of nocturnal habits, like the owl. It should be understood there is really no such thing as true nocturnal vision, i.e., vision in absolute darkness, since the necessary condition for external objects to be seen is that they emit or reflect rays of light which can reach the eye. Animals with diurnal vision can see objects if these objects are sufficiently illuminated, whereas animals with crepuscular vision can see objects emitting an amount of light which could not be perceived by those with diurnal vision. It follows, therefore, that the difference between these two kinds of vision fundamentally depends on the sensibility of the retina to varying degrees of illumination, i.e., on what is called the light sense of the individual considered. In animals with crepuscular vision, the light sense is highly developed and the retina is stimulated by an amount of light which would be insufficient to act upon the retina of an animal of diurnal habits.

**Diverticulum.** A small pouch or sac springing from a main structure.

**Efferent** means carrying from. In the case of nerve fibres the term applies to those fibres which transmit impulses from the brain centres to the peripheral organs, chiefly the muscles. It is equivalent to centrifugal and is often replaced by the term motor, though this is not strictly correct since all efferent fibres are not distributed to muscles but may end in other organs, e.g., a gland, the secretion of which is stimulated by the impulse brought to it through an efferent fibre.

**Emphysema** is a condition in which there is air (or some other gas) in normally airless tissues or again in which there is an excess of air in tissues normally containing a certain quantity of it. Cutaneous emphysema is due to the presence of air in the loose connective tissue beneath the skin.

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**Empyema** means a collection of pus in a cavity of the body (e.g., the pleural cavity) or a similar collection which burrows its way in various other parts, for instance, the subcutaneous tissue.

**Endothelium.** The lining membrane of serous, synovial and other internal surfaces. The term may be regarded as equivalent to internal epithelium. Thus, we call corneal endothelium the thin layer covering the internal surface of the cornea and separating this structure from the aqueous fluid.

**Energy.** The capability of producing work. A stone on the ground does not exhibit any existing energy, but if carried to the roof of a house and allowed to drop to the ground, it may produce mechanical work in breaking an object on which it falls, or it may penetrate more or less deeply into the ground, or again, if the surface of the ground on which it falls is sufficiently hard, the stone suddenly arrested in its fall exhibits an increase in its temperature. Thus by the act of carrying the stone to a high level, which implies work applied to it, it acquires by reason of its position what is called potential energy the amount of which is strictly equivalent to the work spent to carry it to its position on the roof of the house. If the stone is allowed to fall from its raised position it gives up its energy, as shown by the mechanical work it does or by the heat it has acquired.

The amount of heat produced by the stone striking the hard ground is necessarily small and difficult to appreciate, but everybody knows that if a bullet is fired from a gun and strikes a plate of hard steel, the bullet, suddenly arrested in its journey through space, may become red-hot. The energy stored up in the form of potential energy in the explosive used to propel the projectile is transformed into heat. Had the steel plate been less hard, a portion of the energy carried by the bullet would have been spent in penetrating more or less deeply into the plate, i.e., would have been partly transformed into mechanical work.

Any moving body thus possesses what is called kinetic energy and this energy, which is equal to the energy spent in putting the body in motion, can be made manifest by producing mechanical work or by an increase of temperature.

The notion of energy and the law of conservation of energy are the leading principles forming the keystone of modern physical science. The conception of energy, derived in the first instance from the ability of the muscles of the body to do mechanical work, received a quantitative definition from a consideration of the work done in simple mechanical instances. When a weight has to be raised the effort involved depends both on the magnitude of the weight and on the height through which it has to be raised. If we set the effort as being proportional to each of these quantities, the proper measure of it becomes the product of the weight by the height; this product may be described as the energy spent to raise the weight or as the work done by the weight if allowed to fall back in its original position. The accuracy of this mode of reckoning is borne out by many facts.

If the action of some simple mechanical device like a lever or a set of pulleys is carefully studied, it is found easy to arrange that a small weight by falling shall raise a larger one, but it can be seen that the small weight has to descend through a distance greater in proportion, so that really the machine used is incapable of giving out more work than is put into it, work being defined as above. Hence, though a machine may render the work more convenient in form, it is still necessary to make the same effort, i.e., to spend the same

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amount of energy in lifting the weight as without the machine. This result was found to be general and to apply to all machines, but in the search after an exact conception of this thing that appears to be unchanged in mechanical actions, a difficulty arose. While it was not possible to get more work out of a machine than was put into it by any ingenuity of arrangement, actually machines gave out somewhat less work than was put into them. This loss of work is easily traced to the imperfections of the machines, friction being the chief mechanical imperfection. If, however, the loss of work could not be traced further, the conception of energy would be of little use, but it has been found that whenever friction occurs in a machine heat is produced, and this has led scientists to look for the lost work in a production of heat. It results from the researches of Rumford (1800) and of Joule (1840) that when heat is produced by an expenditure of work, the quantity of heat evolved is in strict proportion to the work spent. Further, it was found that work can be produced by the expenditure of heat, as is obvious from the action of a steam engine where the heat of the furnace is the direct cause of the ability of the machine to do work. Finally, it was proved that heat and mechanical work are interchangeable quantities measurable in terms of a common unit and may be regarded as merely two aspects of a common quantity, namely, energy. If we add to this the fact that many other forms of energy are known which may be converted into mechanical work and back again (e.g., the energy of a compressed gas, of a bent spring, of an electric current, of chemical affinity, and so on), we arrive at the conception of energy as a common reality underlying these various phenomena and binding them together, as a quantity remaining fixed and merely passing from one of its forms into another in all the phenomena of the physical world. This is the law of conservation of energy which may now be regarded as an axiom pervading all phenomena of modern science.

**Enophthalmia** (or **Enophthalmos**). Recession or sinking of the eyeball into the orbit. It is often observed after long debilitating diseases when the store of orbital fat has been used up for the purpose of nutrition and is no longer sufficient to maintain the eye in its normal condition.

**Eumatria.** The exact amount of muscular effort to be put forth to accomplish a certain result.

**Evolution.** Strictly speaking, Evolution is the process of developing from a simple to a complex, specialised, and more perfect form. (See Ontogeny and Philogeny).

**Exophthalmic goitre** (or Graves's Disease). A disease characterised by cardiac palpitations, goitre and exophthalmia, the palpitations being usually the initial symptom.

**Exophthalmos** (or **Exophthalmia**). Abnormal protrusion of the eyeball which may be due to the mechanical action of an intraorbital tumour or by an excessive development of the fat filling the retrobulbar part of the orbit.

**Exudate.** The material which has passed through the walls of the blood-vessels into the adjacent tissues.

**Flexure.** A bending. The cervical or cephalic flexure is the arching over the front part of the embryo brain.

**Follicle.** The term generally applies to a small lymphatic gland the tissue of which is arranged in the form of a little sac, and also to a

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single and small tubular gland. A hair follicle is a glandular sac from which the hair grows by proliferation of the cells lining the inner surface of the sac. Removal of a hair (epilation) without destruction of the hair follicle will be followed by the growth of a new hair. At the root or follicle of each hair a sebaceous gland is found, the duct of which empties the fatty secretion of the gland in or about the hair follicle itself.

**Fossil.** Literally—a thing dried up. The term applies to any organic body living in prehistoric times which, being buried in the ground, has been preserved to a more or less complete extent.

**Fundus.** The appearance of the internal surface of the posterior part of the eyeball when viewed with the ophthalmoscope.

**Ganglion.** In connection with our work, the term applies to a well defined collection of nerve cells forming a subsidiary nerve centre. We have alluded to the ganglion on the posterior root of each spinal nerve (page 44) and to the ophthalmic ganglion (page 322).

**Genus,** a Latin word denoting a species or collection of species having in common characteristics differing greatly from those of other species.

**Grave's Disease.** (See Exophthalmic goitre.)

**Hemiplegia.** Commonly called a stroke. Paralysis of one side of the body usually due to an extensive lesion of the cerebral cortex or a lesion of the cerebral peduncles, the pons or the bulb (i.e., the upper part of the spinal cord). If in the brain, the lesion occurs on the side opposite to the paralysis.

**Homologous.** Having a similar structure; of the same make-up.

**Homology.** Correspondence in structure either directly or as referred to a fundamental type. Thus we speak of the homology of the upper limb and the lower limb, the thigh corresponding to the upper arm, the leg to the forearm and the foot to the hand.

**Hemorrhage** (or Hæmorrhage) is an escape of blood from the blood-vessels into the surrounding tissues, either by diapedesis through intact walls, or by rupture of the walls of the blood-vessels.

**Hyaloid** generally means transparent, glass-like. The hyaloid membrane is the delicate transparent membrane surrounding the vitreous humour.

**Hydra**—a small fresh water animal belonging to the same class as Sponges, Jelly-fish, Sea Anemone, etc., i.e., to the class termed Cœlenterates (Cœlenterata). (See Classification of Living Beings.)

**Hyperplasia.** Excessive formation of tissue; an increase in the size of a tissue or an organ owing to an increase in the number of the anatomical elements (cells or fibres).

**Imbibition.** Generally speaking the term applies to the act of sucking up moisture. It is commonly used in a more restricted way and denotes the passage through the thin walls of the capillary vessels of the liquid part of the blood which thus exudes into the surrounding tissues and presides to their nutrition. In its physiologic sense the term is practically equivalent to osmosis.

**Inhibition** means in a general way, a restraint or the act of checking or restraining. (Synonymous with Frenator).

**Intercalar.** A part placed or inserted between two existing parts.

**Iridodonesis.** A trembling of the iris.

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**Iridodyalisis.** Separation of the iris from its attachment to the ciliary body.

**Irritability.** The property or power of a living cell of responding to a stimulus.

**Lamella**—a thin scale or plate. We have alluded to the lamellæ in the form of concentric rings surrounding the Haversian canals of bones.

**Lamellar.** Having the nature of or resembling a thin plate, or again, a structure composed of lamellæ or thin layers, e.g., the lamellæ of the substantia propria of the cornea, or the concentric laminæ constituting the crystalline lens.

**Lamina**—a single thin plate or layer. The lamina vitrea is the thin vitreous or glass-like structureless membrane covering the inner surface of the choroid and separating this structure from the retina; it is often called the membrane of Bruch.

**Larva.** The first condition of an insect as it is issuing from the egg, usually in the form of a grub or caterpillar.

**Larynx.** The upper part of the wind-pipe or trachea differentiated for the production of the voice. It is a cartilaginous structure, the fundamental part of which consists of two prominent processes of the mucous membrane lining it (the vocal cords) which are stretched across the larynx cavity and are capable of vibrating under the action of a current of air proceeding from the lungs.

**Law.** A law is a generalised statement of facts, a general rule or constant mode of action of forces or phenomena. The two main laws which form the basis of physical science, in the broadest sense of the term, are the Law of Indestructibility of Matter and the Law of Conservation of Energy. We can transform matter from one form into another but we cannot destroy it. For instance, when a piece of coal is burnt it apparently disappears, leaving a slight residue of mineral incombustible matter or ashes, but the coal has not really disappeared; it has entered into a combination with the oxygen of the atmosphere to form carbonic acid gas and a careful analysis shows that the amount of carbon existing in the original piece of coal in association with a variable amount of incombustible material (remaining as ashes) is found in the carbonic acid gas which is the result of the oxydation or combustion of the carbon. The Law of Conservation of Energy is dealt with under the heading of Energy.

The Law of Topographic Homology applies to the situation in a section of the optic nerve of the fibres proceeding from the various parts of the retina; it expresses the fact that the different regions of the retina correspond, point by point, to the corresponding regions of the transversal section of the optic nerve on the same side and of the optic tract on the opposite side. Thus, the external region of the right retina sends its fibres to the external part of the right optic nerve and to the internal part of the left optic tract. The only apparent exception is that of the papillo-macular bundle which, on leaving the globe, occupies the infero-external part of the optic nerve exactly as in the retina the macula occupies the infero-external portion of the membrane. However, the papillo-macular bundle soon passes into the central part of the nerve and keeps this position in the nerve, the chiasma and the tract. The Law of Topographic Homology applies to the whole of the visual path as is explained in Chapters XIII. and XIV.

**Ligament.** A ligament is a band of flexible, compact, connective tissue uniting the articular ends of bones in a joint and sometimes

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enclosing them in a capsule. The pectinate ligament which has been fully described in page 200 is the spongy tissue at the junction of the cornea and sclerotic. It forms the root of the iris and the spaces or meshes in it constitute what we have termed the filtration angle.

**Locomotor Ataxia.** (See Ataxia).

**Matter** denotes that of which all things are made, or, in other words, it means all things we can recognise or perceive by our sense-organs. It is a well known fact that matter in mass, i.e., in large pieces, may occur in solid or liquid or gaseous form. Further, any mass or piece of matter is made up of very small particles called molecules and, in their turn, molecules are made of atoms.

The divisibility of matter has been much discussed by philosophers, and as far back as the time of Lucretius it had been recognised that this divisibility is limited. Thus, if we take a piece of common salt, we can break it into smaller and smaller bits and though, theoretically, this process of breaking could be carried out indefinitely, yet chemical researches show, in an absolutely certain manner, that by successive division we can arrive at the smallest possible particle having in itself all the properties of common salt. This smallest particle of salt is what we call the molecule. Of course, we cannot expect to see a molecule even with the most powerful microscope, but we can arrive at the notion of the molecule in other ways. By purely mechanical means we can divide a bit of common salt until we reach a particle nearly 1-4,000th of a millimetre in diameter, which is about the smallest size of anything visible under the microscope. We have good reasons for believing that such a small particle possesses all the known qualities of salt. But we can go farther and dissolve a small amount of salt in water; no microscope will then show any visible part in the solution though each drop of the solution would taste " salt " and exhibit all the chemical properties of salt. Moreover, by evaporation or boiling up of the water, we can recover the salt unadulterated. Hence we can conclude that when in solution the salt is divided into particles of ultra-microscopic size we call molecules. Hence, there is a certain small mass of salt, the molecule, which is the least possible mass exhibiting all the properties of common salt.

By chemical means, however, we can find that the molecule of common salt is made of two other substances, namely, a green poisonous gas (chlorine) and a soft metal called sodium. It is for this reason that common salt is called sodium chloride.

The word molecule is derived from the Latin and means a small mass or quantity. There are in the universe various substances (nearly 90 in all) which have never been resolved or decomposed into any other substances, and these are called elements. The smallest possible quantity or mass of any element which can exist as such and exhibit all the properties of the substance considered is called an atom of it. Hence, the molecules of complex substances are built up of atoms held together so as to form similar bunches or groups. In certain very simple compound substances, like ordinary salt, the molecule may consist of only two dissimilar atoms, but in organic substances, like albumin, fats, oils, starch, etc., the molecules may contain many scores of atoms.

Even in elements, such as hydrogen or oxygen, the constituent molecules contain two similar atoms held together. The fact that small definite units called atoms exist in the molecule of the various elements is supported by the three fundamental laws of chemistry,

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namely, the law of definite proportion, the law of relative proportion, and the law of multiple proportion. We cannot enter into details in the subject of these laws, and refer the reader to any modern text-book on Chemistry.

In ancient times, scientists thought that there were four elements, namely, earth, fire, air and water; it is known now that none of these is really an element according to the definition given above.

The various elements have different chemical powers, i.e., when they combine with each other, they have different capacities. Thus, hydrogen is an element with the lowest combining power which is generally taken as being unity. Oxygen, compared with hydrogen, has twice the combining power of the latter and its power is therefore represented by two. Carbon has a combining power represented by four, and so on. If we think of an atom of hydrogen as a minute ball fitted with a single hook, we must think of the atom of oxygen as a ball with two hooks and of the atom of carbon as a ball with four hooks.

On combining an atom of oxygen with two atoms of hydrogen, the two hooks of the former being linked with the single hook of each atom of hydrogen, we arrive at the molecule of water, chemically represented by $H_2O$.

Likewise, a single atom of carbon with four hooks can be linked with four separate atoms of hydrogen, giving rise to the compound called methane, the constitution of which is represented by $CH^4$. Or again, a single atom of carbon (with four hooks) can be linked with two separate atoms of oxygen each of which has two hooks, the result of the combination being carbon dioxide or carbonic acid gas $CO_2$.

This rough comparison explains what is termed the valency of each element. The atom of hydrogen is monovalent since it can be regarded as a ball with one hook; the atom of oxygen is bivalent, that of carbon tetravalent.

As regards the size of atoms and molecules, there are various lines of argument leading to the conclusion that, roughly speaking, the size of an atom is of the order of one hundred millionth of a centimetre, which means that if a million atoms were placed in contact like a row of marbles they would only occupy a length of 1-10th of a millimetre, or less than the thickness of the thinnest sheet of tissue paper. To count this million would take about a week, counting without stopping, day and night. Non-scientific persons are apt to imagine that such figures are mere guesswork, but such is not the case, and it is possible, by various methods into the details of which we cannot go, to count the number of molecules in, say, a cubic inch of air with as close an approximation to truth as we can reckon the number of men, women and children in Great Britain by a census taken at any fixed date.

An approximate measurement of atomic diameter is derived from the study of thin films of various kinds. A skilled gold beater can beat out one ounce of gold until it covers an area of 240 square feet. The thickness of the gold sheet would then be about four millionths of an inch or one sixteen thousandths of a millimetre, or one sixteenth of a micron. (See micron and other units for the measurement of very small lengths.)

It is comparatively easy to prepare gold leaf the thickness of which is one tenth of a micron. Such leaf when held up to the light appears semi-transparent and transmits green light. This gold leaf has, however, several hundred layers of atoms, probably 300 to 500. We can prepare thinner films of soapy water. If a soap bubble is



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blown with a tube or, still better, if a metal ring is filled with a soap film by dipping it into the soapy mixture, and this film is placed in a dust free glass box in a vertical position, the film begins to thin away by drainage from the top part. Presently, we will notice in it small round black spots which look like holes but are not holes since in proper position we can see an image of a bright object, say, the sun, formed by reflection at the surface of the so-called hole. It is possible by various ways to measure the thickness of the film in these black spots. It is found to be about 60 A.U. or six thousandths of a micron. Yet the film must be of a thickness equal to the diameter of several atoms. The late Lord Rayleigh measured the thickness of still thinner films of oil floating on water and found it to be about 20 A.U. More recently, Devaux produced films of oil on water of about half the above thickness, i.e., 10 A.U., and he came to the conclusion that this film was probably due to a single layer of molecules of oil. This, and many similar results obtained in other ways, led to the conclusion that molecular diameters must be of the order of one hundred millionth of a centimetre or from one to five times the size just stated.

**Medulla.** The term is used in different ways. It denotes the portion of the cerebro-spinal centres between the spinal cord and the brain proper (medulla oblongata or bulb). It is also occasionally applied to the marrow of bones. In connection with our work the term is chiefly used to denote the insulating coating of the cylinder-axis of a nerve fibre, this coating being made of a white, highly reflecting substance termed myelin.

**Metabolism.** The group of phenomena whereby living beings transform foodstuffs into complex tissue elements (constructive metabolism or assimilation or anabolism) and convert complex substances into simple ones in the production of energy (destructive metabolism or disassimilation or katabolism).

**Mimicry** (literally imitation). It frequently happens, amongst animals, that a particular species is found to resemble in outwards appearance not its own immediate allies, but some other unrelated form. For instance, a special form of butterfly living in South America shows remarkable resemblance to another form. The latter possesses an offensive smell and taste which renders it obnoxious to insectivorous animals, and it is probable that the resemblance between the former and the latter is calculated as a means of protection. To this kind of protective resemblance, the term mimicry has been applied. The white fur of the foxes, bears, etc., living in Arctic snow-covered countries, is also no doubt a phenomenon of mimicry intended to render the animals less conspicuous to potential enemies, though it may partly be accounted for as being a means of defence against the insufficiency of the solar radiations.

**Molluscs** (Mollusca) constitute a large series of invertebrate animals including such forms as snails, slugs, oysters and mussels, together with the different species of cuttle fish. They differ from arthropodes and worms by the absence of segmentation of the body, and by the fact that most of them have an outside shell made of one or two valves serving as a protection, a kind of outer skeleton. (See Classification).

**Monster.** In physiological and medical work the term monster applies to an individual who, by reason of congenital faulty development, is incapable of properly performing the vital functions or who, owing to an excess or a deficiency in the development of some parts of the body, differs in a marked degree from the normal type of the species.

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**Morphology.** The branch of science concerned with the study of the form and structure of living beings.

**Myelin.** (See Medulla.)

**Natural Selection** is one of the factors bearing on the evolution of living beings generally. To explain the numerous forms of animal species which have succeeded each other during the various geological periods and have given rise to those species actually in existence, there are only two possible theories. The first is that all living beings are due to the Creator and perpetuate themselves while keeping their primitive characteristics. This theory, which is termed the theory of fixed species, has mostly been supported by Cuvier. According to the second theory, the various animal and vegetal species existing at present derive from more ancient and simpler forms which, in the course of centuries, have undergone gradual transformations; the starting point of all living beings existing at present is the simplest form of living cells, represented by the amœba and several other unicellular organisms. This second theory is called Evolution or Transformism, and more often Darwinism, from the name of the scientist (Darwin) who gave a clear account of it in his immortal book on the Origin of Species (1859). The basis of the evolution theory had been advanced before Darwin by several scientists, especially Lamarck and Geoffrey Saint-Hilaire (about 1794) but it was not generally accepted by the scientific public of the time whose mind was badly prepared for such a brilliant conception and was greatly influenced by the arguments advanced by Cuvier in defence of his theory of the fixity of species.

The main factors in Evolution are: (a) The adaptation of organs to surrounding circumstances, with the consequent use of certain organs and the disuse of other ones which have become useless in the circumstances in which the living being is placed; (b) the struggle for life or natural selection. Darwin has borrowed the principle of this theory from the English economist, Malthus. According to Malthus, if a human community lives in a limited area of country, the number of living persons increases in geometrical progression while the quantity of substance necessary to keep them alive and derived from the soil only increases in arithmetical proportion. It follows that, after a number of generations, the population will be too great for the quantity of nutritive matter at their disposal. When this stage is reached a true struggle is bound to occur between individuals for the sharing of the food; those who, for any reason, are weaker than others and less apt to procure their share of food or are less resisting to various causes of destruction (cold, enemies, parasites, climatic conditions, etc.) are bound to disappear, while the strongest, more resisting, and better fitted for this struggle for life will survive. This is an instance of natural selection. According to Darwin, this selection plays its part in the series of successive generations and only allows the more robust specimens to survive, those who are more apt to live in the condition of the moment and adapt themselves best to the surrounding circumstances. Those species which have disappeared as the result of the struggle for life are often found in the state of fossils.

**Necropsy.** The examination of a dead body. Equivalent to autopsy or post-mortem examination.

**Necrosis** (from the Greek *necros*, meaning death). Death of cells surrounded by living tissues. Necrosis proper refers to death in mass; necrobiosis, to death of individual cells. Amongst the causes of necrosis are: direct injury, obstruction of the circulation, and loss of

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nutrition. Necrosed tissues may be absorbed, retained or thrown off. The dead tissue is called sequestrum in the case of bone, and sphacelus or slough in the case of soft parts (e.g., the slough of a boil or furuncle, i.e., of a localised inflammation of the skin and subcutaneous tissue attended by the formation of pus).

**Necrotic.** Pertaining to, or characterised by, necrosis.

**Nephritis.** (See Albuminuria.)

**Neuraxon.** (See Axis-Cylinder.)

**Neuritis** means inflammation of a nerve. Optic neuritis is inflammation of the optic nerve. Multiple neuritis is the result of simultaneous inflammation of several nerve trunks usually symmetrically situated on both sides of the body.

**Neuroglia** (or nerve-glue) is a tissue, of ectodermic origin, which forms the basis of the supporting frame work of the true nervous elements (nerve cells and nerve fibres) in the cerebro-spinal centres and in some sensory epithelia, e.g., the retina. It consists of peculiar small cells having many fine branched and wavy processes.

**Neuron.** The histological and functional unit of the nervous system. A neuron consists of a nerve cell with all its processes, namely, the dendritic or branched processes and the axon which does not branch and is continued into the cylinder-axis of a nerve fibre. Neurons are joined together not by material continuity but by contiguity. If we imagine the branches of two adjacent trees freely intermingling we have a rough picture of the interconnection of two neurons. When the dendrites of a neuron form a network in close proximity to, or even surround the body of an adjacent neuron, this network which insures contiguity but not structural continuity, is called an arborisation or a synapse. Thus, in the retina the first visual neuron consists of a cellular body, the rod-granule or cone-granule, the outer protoplasmic process of which is differentiated so as to assume the form of a rod or a cone. The axon of the cell is directed inwards constituting the rod-fibre or the cone-fibre and ends in the terminal knob for a rod and in the cone-foot for a cone. This first retinal neuron is followed by a second one in which the cellular body is a bipolar cell the outer processes of which form an arborisation or a synapse with the terminal knob or the cone-foot of the previous neuron according as the bipolar cell considered is related to a retinal rod or a retinal cone. The third visual neuron (partly retinal, partly orbital and partly intercerebral) has a ganglionic cell as cellular body. The dendrites or outer processes of these cells form synapses in the same way as stated above with the axons of the corresponding bipolar cell, while the axon of each ganglionic cell is continued into an optic nerve fibre which ends in the primary visual centre, namely, the external geniculate body.

The main point to bear in mind is that the various neurons are not in structural continuity but this does not prevent the physiological continuity that is necessary to the transmission of nervous impulses. To use a rough comparison, we could assimilate the synapse of neurons to what happens when an electric current is transmitted, not by a continuous wire, but by a metallic chain; though there is not continuity of metal, yet the current is transmitted through the mere contiguity of the various links of the chain.

**Ontogeny.** The study of the development of man or of any type of animal as an individual organism. The term is practically synonymous of **Embryology.**

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**Osmosis** (endosmosis and exosmosis) generally denotes the passage of a liquid through a porous wall or membrane from without inwards and from inside outwards respectively.

**Ossification.** The formation of bone from pre-existing cartilage.

**Paleontology.** The branch of natural science devoted to the study of ancient living beings (now extinct) or of fossils.

**Paralysis.** A loss of motion or of sensation in a part of the body.

**Paresis.** A slight paralysis, i.e., a partial loss of motion or of sensation in a part of the body.

**Pathogenic** or **Pathogenetic** is the term used to denote any process causing disease.

**Pathology** is the branch of medical science which is concerned with the modifications of functions and the changes in structure caused by disease.

**Pelvis.** The ring formed by the bones (ischium, ilium and pubis) which are articulated to the lower part of the vertebral column and constitute together what is often termed the hip bone. The ilium has a hollowed cup-like cavity, the acetabulum, which lodges the head of the femur or thigh bone, the whole arrangement constituting the hip joint.

**Pharynx.** The part of the alimentary canal between the palate or the mouth and the œsophagus or gullet. It serves as an air passage from the nasal cavities and the mouth to the larynx in addition to being a food passage from the mouth to the gullet.

The pharynx or the back of the mouth is an irregular cavity 5 or 6 cms. wide and about 10 cms. long, into the front part of which the two nasal cavities and the trachea (or windpipe) open while the gullet or œsophagus opens farther back and carries the food into the stomach.

It is important to understand how the food as it is swallowed passes into the gullet and escapes the orifices of the air passages. The upper part of the windpipe, i.e., the larynx, is fitted with a vertical cartilaginous membrane situated at the posterior end of the tongue and called the epiglottis. Moreover, another membrane of muscular nature, the soft palate or velum, forms the roof of the pharynx and closes the openings of the nasal cavities. The middle of the soft palate is prolonged into a little hanging structure called the uvula. The sides of the soft palate skirt the passage and form a double muscular pillar, the fauces, between which the tonsils are situated, one on each side. The food masticated in the mouth is collected into a small soft ball which slides over the tongue. At the same moment the whole larynx is raised up by the action of special muscles so as to be closed by the back of the tongue and the epiglottis turns round so that the ball of food reaches its upper surface and passes into the gullet without entering the larynx. Simultaneously, the soft palate contracts and together with the uvula, assumes a horizontal position which closes the orifices of communication with the nasal cavities. The loss of the epiglottis or its paralysis does not appreciably interfere with the act of swallowing, because the larynx is sufficiently closed by the base of the tongue as it is raised, as stated above, but the deglutition or swallowing of liquids may be somewhat difficult.

**Phenomenon** (plural, phenomena). The term was at first used to denote any unusual or remarkable appearance, but now, and in a more general way, the word phenomenon applies to all the changes which occur in the universe and are perceived by observation or experiment.

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**Phylogeny.** The study of the evolution of man and generally of the various animal forms from which the human organism has been developed in the course of countless ages. It is mainly due to the publication of Darwin's Origin of Species (1859) that Phylogeny (i.e., the branch of science which described the ascent of man from the lower ranks of the animal world) is born. The chief source that Phylogeny draws upon is Ontogeny and Embryology, i.e., the science of the development of the individual organism. Moreover, it derives a good deal of support from Paleontology or the science of fossil remains of animal types now extinct, and even more so from comparative anatomy.

**Plasma.** The fluid part of the blood and the lymph.

**Plexus** (from the Latin *plectare*, to knit). A network made of an aggregation of blood-vessels (vascular plexus) or an aggregation of nerve fibres forming what is called a nervous plexus.

**Plica**—a fold. The plica-semilunaris is a conjunctival fold in the inner canthus of the eye and represents a rudiment of the third lid or nictitating membrane found in birds and many animals.

**Process.** The term has two different meanings; it applies to a course of action, a group of phenomena, e.g., the process of digestion, or a pathological process. It also applies to a prominence, or an outgrowth of some parts of the body; for instance, the axon of a nervous cell is a process originating from the protoplasm of the cell body and is generally continued into the cylinder-axis of a nerve fibre. We have also alluded to the protoplasmic processes or pseudopodes of an amœba and to the dendritic processes of a nerve cell.

**Protoplasm.** The viscid material constituting the main substance of a living cell upon which all the vital functions of nutrition, secretion, movement, growth, reproduction and irritability depend. Viewed under a microscope with a high magnification, the protoplasm of most cells appears as a network (or spongioplasm) containing in its meshes a more fluid substance termed the hyaloplasm.

**Radiations.** The Universe does not merely consist of the solid, liquid or gaseous bodies we know through our sense-organs. According to a hypothesis generally adopted there is a very subtle, imponderable medium, termed ether, which escapes our most accurate means of observation and pervades all space, at least up to the most distant stars. Not only does this medium fill what we term vacuum, the vacuum of interstellar spaces as well as that we can produce with our best pneumatic machines, but it also penetrates, without any difficulty, all material bodies, even the most compact; to use a somewhat rough comparison, ether flows through material bodies, as water passes through a net or air through a fine gauze.

This medium, ether, which must have a considerable elasticity, is able to vibrate, and the vibrations produced at any point are transmitted in all directions in vacuum as well as in material bodies as ripples or waves are produced and propagated when a stone is dropped into a pond of water; these ethereal vibrations constitute what is termed radiations.

This propagation of vibratory movement corresponds to the transfer of a certain amount of energy which, in certain conditions, may be transmitted wholly or partly to material bodies, and these bodies undergo modifications which differ from one another, not by their cause which is the same, namely, energy, but by the nature of the

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reactions these bodies are capable of exhibiting, according to their constitution or to the conditions in which they are placed.

Without entering into details which are beyond the scope of this book, we will state that all material bodies are made of molecules which are not in contact with one another but which oscillate round each other with an enormous velocity that depends on the temperature of the body. It is this vibratory movement which is the source of molecular kinetic energy and it is only at the temperature physicists call the absolute zero that the molecular movement is stopped. The absolute zero corresponds to −273° C. If a body, for instance, a gas, could be cooled to that temperature, it would have no pressure since it would have no kinetic energy, no heat.

If we raise the temperature of a body, i.e., if we spend a certain amount of energy on it, and provided this does not cause it to undergo a chemical decomposition, we increase the rate of its vibratory molecular movement and thus a wave motion of same frequency is set up in the surrounding ether; this ethereal wave motion carries the energy of the vibrating body in all directions. Assuming the body under experiment is a small length of platinum wire, and that the energy spent on it is that derived from an electric current of variable intensity, it will be found that so long as the temperature of the wire is less than about 400 or 500° C, nothing apparently occurs except that the wire is distinctly hotter than it was at the ordinary temperature. In other words, bodies at ordinary temperatures do not emit radiations which affect the eye, but at a temperature of 400 or 500° C they begin to emit radiations corresponding to the infra-red or calorific part of the of the spectrum, radiations which can be detected by sensitive thermometers. If, by increasing the intensity of the electric current, the temperature of the wire reaches about 700° C, the wire itself will appear red-hot, i.e., will emit visible radiations giving to the average human eye the sensation of red. The spectrum given by the light of the wire would then be reduced to a small piece corresponding to the extreme red of the ordinary solar spectrum. As the temperature of the wire is further increased beyond 700° C, the spectrum obtained will gradually extend to the orange, then to the yellow, then to the green and ultimately to the violet, so that at a sufficient temperature the luminous body emits radiations giving to the eye the simultaneous sensation of red, orange, yellow, green, blue and violet, i.e., the sensation of white light; the luminous wire has become white hot.

When the ethereal waves set up by the vibratory molecular movements of material bodies strike the retina of an eye, or a photographic plate, or a highly sensitive thermometer, they produce, according to their wave-length, a sensation of light, or they act on the photographic plate, or they produce an increase in temperature shown by the thermometer. Thus sensations of light result from the actions of ether waves of a proper wave-length upon the sensitive elements of the retina; but the old belief that the sensation was primarily due to a series of mere mechanical impulses or beats, just as a sound results from the mechanical impact of air waves upon the sensitive organs of the internal ear, cannot any longer be upheld.

The famous researches of Hertz have established upon a secure experimental basis the hypothesis of Maxwell that light is an electromagnetic phenomenon. Such electric radiations as can be produced by special instruments and are used in wireless telegraphy are found to behave in exactly the same way as those to which light is due. They travel through space with the same velocity, they can be reflected, refracted, polarised, and made to exhibit interference effects. No fact

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in physics is much more firmly established than that of the essential identity of light and electricity. It follows that the displacements of ether which constitute light waves are not necessarily of such a gross nature as those which we see on the surface of water, or which occur in the air when a sound is transmitted through it. The displacements which the ether undergoes are not mechanical, primarily at all events, but electrical.

Everyone knows what a simple mechanical displacement is; the vibration of a pendulum gives a good example of such a displacement. But if we electrify a stick of sealing wax by rubbing it with flannel, the surrounding ether undergoes electric displacement; the exact nature of this phenomenon is not known, but ultimately, no doubt, it will be found to be of a mechanical nature, though it is almost certainly not a simple bodily distortion such as is caused, for instance, when one presses a jelly with the finger.

The existence of a universal medium capable of transmitting at the enormous speed of 186,000 miles or 300,000 kms. per second, disturbances which, whatever their real nature, are of the kind mathematicians call waves, had been postulated by Newton as a physical necessity. The existence of ether is now firmly established, though the essential nature of the action produced by ether waves on the eye is not yet ascertained. Many guesses at the truth have been hazarded and the effect of ether waves on the eye may be electrical or chemical, or both. Ether waves, we know, are competent to bring about chemical changes, as in the familiar example of the photographic plate; they can also produce electrical phenomena as, for instance, when they fall on a suitably prepared selenium cell, but there is no evidence that they can exert any direct mechanical action of a vibratory character, and, indeed, it is barely conceivable that any portion of our organism should be adapted to take up vibrations of such enormous rapidity as those which characterise light waves.

Of the multitude of ether waves which traverse space it is only comparatively few that have the power of exciting a sensation of light. As regards this limited range of sensibility, there is a close analogy between hearing and seeing. No sensation of sound is produced when air waves beat upon our ear unless the rate of the successive impulses lies within certain definite limits. It is just so with vision. If ether waves fall upon our eyes at a less rate than about 420 billions per second, or at a greater rate than 750 billions per second, no sensation of light is perceived. The same fact may be stated in another and more convenient way. Since all waves that are propagated in ether travel through space at exactly the same speed, namely, 300,000 kms. or 30,000,000,000 cms. or $3 \times 10^{9}$ cms. per second it follows that the length of each of a series of homogeneous waves must be inversely proportional to their frequency, i.e., to the rate at which they strike a fixed object such as the eye.

Instead, therefore, of specifying waves by their frequency we may more conveniently specify them by their length. Waves whose frequency is 420 billions per second have a length which is the four-hundred twenty billionth part of 300,000 kms., i.e. (if expressed in mms.) of 0.000712 mms. To express such small lengths, the millimetre is too large a unit; even the micron, i.e., the thousandth of a millimetre, denoted by the Greek letter $\mu$, and used as unit of length for microscopic objects, is still too large. It is the custom to express wave-lengths in milli-microns, denoted by $\mu\mu$; a milli-micron is one-thousandth of a micron or a millionth of a millimetre. Hence the wave-length of those waves whose frequency is 420 billions per second

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is 712$\mu\mu$. Some authorities take as unit the tenth of a milli-micron which is called the tenth-metre or Angstrom unit, denoted by the initials A.U. A wave-length of 712$\mu\mu$ is 7,120 tenth-metres or 7,120 Angstrom units, generally written 7,120 A.U.

In the same way ether waves the frequency of which is 750 billions, have a wave-length of 390$\mu\mu$ or 3,900 Angstrom units. Waves of a length greater than about 7,120 A.U. or less than 3,900 A.U., have no effect upon our organ of vision. Wave-lengths of about 7,120 A.U. give rise to the sensation of red, those of about 3,900 A.U. to the sensation of violet. Intermediate wave-lengths give rise to the coloured sensations between red and violet.

The position of the boundaries of the visible spectrum in the classical experiment of Newton does not depend upon anything whatever in the nature of light regarded as a physical phenomenon. Ether waves which are much longer and much shorter than those which correspond to the visible spectrum certainly exist, and evidence of their existence is supplied by their effect on a sensitive thermometer in the case of the former, and by their effect on a photographic plate or on photographic paper in the case of the latter. Such waves, however, fall upon our eye without exciting the faintest sensation of light.

The visible spectrum is limited solely by the physiological constitution of our organs of vision, and the fact that it begins and ends where it does is, from the physical standpoint, a mere accident. The main function of the ether in the economy of the universe is to undulate, and to transport energy from one place to another by wave motion. Some of its waves, such as those which are made use of in wireless telegraphy may be many thousands of metres in length, others may be shorter than 100$\mu\mu$ or 1,000 A.U., as is probably the case with those associated with X-rays, but all, so far as is known, are of essentially the same character, differing from one another only as the billows of the Atlantic Ocean differ from the ripples created on the surface of a pond when a stone is dropped into it. No matter how the disturbance in the ether is set up, whether by the sun, or by a dynamo, or by a hot flat-iron, in every case the ether conveys nothing at all but the energy of a wave motion and when the waves, encountering some material obstacle which does not reflect them, become quenched, their energy takes another form and some kind of work is done or again heat is generated in the obstacle. The whole or at least the greater part of the energy given up by the waves is, in most cases, transformed into heat, but under special circumstances, as for instance when the waves fall upon the green leaves of a plant, or a living eye, or a selenium cell, a few of them may perform work and give rise to chemical changes in the leaves, or to a sensation of light in the eye, or to electric phenomena in the selenium cell.

The process of the transmission of energy from a body to another by propagation of a wave motion, through an intervening medium, has long been spoken of as radiation, and in recent years the same term has been largely employed to denote the energy itself while in the stage of transmission. "Radiation" in this sense, meaning ether wave energy, includes what is often called light. One often reads that light travels from the sun to the earth in a little more than 8 minutes, but while on its journey it is not light in the true sense of the word; neither does anything in the nature of light start from the sun. As Prof. Bidwell puts it, "Light has no more existence in nature outside a living body than the flavour of onions has; both are merely sensations."

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If a boy throws a stone which hits you in the face, you feel a pain, but you do not say that it was a pain which left the boy's hand and travelled through space to you. The stone instead of causing pain in a sentient individual might have broken a window or brought down an apple, in which case the muscular energy spent by the boy in throwing the stone would be transformed into mechanical work, or again, if the stone strikes an obstacle which it can neither break nor penetrate, the energy carried by it is transformed into heat as shown by an increase in the temperature of the stone. The amount of heat thus produced by a stone striking an obstacle is small and difficult to appreciate, but everybody knows that if a bullet is fired from a gun and is received on a plate of hard steel, the bullet, suddenly arrested in its journey through space may become red hot; the energy stored in the explosive used to propel the projectile is transformed into heat. Had the steel plate been less hard a portion of the energy carried by the bullet would have been spent in penetrating more or less deeply into the plate, i.e., would have been partly transformed into mechanical work. Just so, the same radiation which, when it chances to encounter an eye, produces a certain sensation will produce a chemical effect if it falls on photographic plates, an electrical effect if it falls on a selenium cell, or a heating effect in almost anything. Why then should it be specially identified with the sensation?

Radiation also includes, and is nearly synonymous with, what is often miscalled radiant heat. After what has been said just now, it is clear that there is no such thing as radiant heat. The sun or any other hot body generates wave energy in the ether at the expense of some of its own heat and any distant substance which absorbs a portion of this energy, generally though not necessarily, acquires an equivalent amount of heat. The result may be the same as if heat had left the hot body and travelled through space, but the process is different. It is like sending a florin to a friend by postal order. You part with a florin and your friend receives a florin, but the piece of paper which goes through the post is not a florin. It is strictly correct to say that the sun loses heat by radiation just as you lose a florin by investing it in the purchase of a postal order. But that is not the same thing as saying that the sun radiates heat.

The term radiation has the advantage of avoiding any suggestion of the fallacy that there is some essential difference in the nature of the ether waves which may happen to terminate their respective careers in the production of light or heat or chemical actions or anything else, but it is, unfortunately, impossible in the present condition of things to use it as freely as one could wish without pedantry, and we must still often speak of light or heat when the term radiation would express our meaning with greater accuracy.

All observations and known facts tend to prove that there is no essential difference between the causes which produce luminous sensations of various colours, those which act on photographic paper, i.e., which give rise to chemical or actinic phenomena, or again those which produce a mere sensation of heat.

All those phenomena are due to radiations and the only difference consists in the various values of the duration of the vibration or, which comes to the same, in the wave-length of these vibrations. We can go further. Apart from the ether waves set up by the molecular vibratory movement of material bodies which give rise to the infra-red, the visible and the ultra-violet radiations, it has been found that when an electric spark passes between two metal balls, ether waves of relatively considerable wave-lengths are set up and transmitted through space;

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it is this kind of wave which is utilised in wireless telegraphy. The shortest wave of this kind which has been obtained has a wave-length of about 3 mms. but powerful sources of electricity, in conjunction with suitable apparatus, can give rise to radiations the wave-lengths of which may reach a very high value, amounting to several thousand metres.

These electric or Hertzian waves (from the name of their discoverer) appear in all respects to be similar to those which give rise to the visible and non-visible spectra, the only difference being in the wave-length or the frequency. They travel through space at the same rate, they can be reflected, refracted, polarised and made to exhibit phenomena of interference.

It follows that the four great groups of ether waves or radiation, namely, the actinic or ultra-violet waves, the visible radiation, the infra-red or calorific waves and the electric or Hertzian waves are really and essentially the same in nature and consist in periodic disturbances or waves, propagated through the ether in every case with a speed of 300,000 kms. per second.

We may, therefore, say that these various classes of ether waves differ from each other only in the same sense in which a deep musical sound differs from a high-pitched one; the difference is merely one of wave-length or frequency.

On the other hand, the curious radiations discovered by Röntgen and termed by him X-rays most probably consist of ultra-violet radiations of extremely short wave-length, and this very peculiarity explains why the radiations in question differ by some of their properties from those of the other groups. For instance, X-rays are easily diffused but not easily regularly reflected. It is a known fact that the smoothness of a surface necessary to produce regular reflection depends on the wave-length of the radiation employed or, more exactly, on the relative size of the wave-length and of the surface irregularities. If the wave-length is appreciably larger than the surface irregularities, there is regular reflection; if appreciably smaller, the waves are broken up by the irregularities or roughness of the surface, and there is diffusion or scattering. For instance, ground glass is not smooth enough to reflect regularly the visible radiations but it does reflect regularly the long infra-red waves because the wave-lengths of the latter are large and those of the former small as compared to the size of the surface irregularities. It is not astonishing, therefore, to find that the exceedingly small wave-lengths which give rise to X-rays cannot easily be regularly reflected but are readily diffused.

**Salamander,** a genus of tailed Amphibians including three different species, all confined to the Old World. The most common species is the spotted or fire salamander found in most parts of Western Europe, five to six inches in length, black in colour with vividly marked yellow spots. The skin bears two series of glands, one on either side, which secrete a white poisonous fluid that is squirted out in fine jets when the animal is irritated. The poison is strong enough to kill a small animal if introduced into its blood or its stomach. The spotted variety of salamander is of terrestrial habits, but requires a moist locality.

The other two species are the Alpine or black salamander and the Caucasus salamander. The former is about the same size as the spotted variety but without the yellow spots; it is confined to the Alps region, in the vicinity of water and at an altitude of two thousand to nine thousand feet. The latter, very similar to the spotted one, is found in the Caucasus. (See Classification of Living Beings).

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**Science** (from the Latin *scire*, to know) is the knowledge of the order of nature as found out by observation, experiment and reasoning. Professor Ray Lankester defines Science as "that knowledge which enables us to demonstrate, so far as our limited faculties permit, that the appearances and phenomena we recognise in the world around us are dependent in definite ways on certain properties of matter." To put it more briefly, Science is the knowledge of the laws governing the forces of nature.

The subject matter of all possible human knowledge is contained in two separate realms, an outer and an inner one; the outer realm or outer world consists of matter, the inner one is what we call generally the mind.

In a broad way Science may be sub-divided into (a) Physical Science which deals with the outer world, the fundamental ideas of which are matter and energy; and (b) Mental Science which deals with the inner world, the fundamental ideas of which are knowing, feeling and willing. The term mind may be defined as that within us which knows, feels and wills.

Just as Physical Science is divided into various branches such as Physics, Chemistry, Mechanics, Physiology, etc., so Mental Science is divided into different branches, the principal one of which is Psychology, which deals with the phenomena of knowing, feeling and willing. Any particular mental activity is called a state of consciousness or a psychosis and Psychology is mainly concerned with the discovery of the relation between different states of consciousness. Psychology does not include the study of what the mind is in itself, but only the study of the various phenomena of the mind and of the relation between them. The branch of Science attempting to explain the real nature of the mind is called Philosophy or Metaphysics, the aims of which are the discovery of the real nature of matter and of mind and of the relation between them.

Though Psychology is the main branch of mental science, there are other branches, such as Ethics (the science of conduct), Politics (the science of government), Sociology (the science of societies), Logic (the science of reasoning), Pedagogy (the science of education), Æsthetics (the science of the beautiful in nature and art), etc.

Physical Science includes Physiology or Biology, i.e., the science of living beings. In ancient times the phenomena occurring in a living organism were attributed to the existence of a vital principle, but modern researches have proved that most of the physiological phenomena take place according to the laws of Physics and Chemistry. Even nervous phenomena are now studied in terms of the physical and chemical laws and recently a new branch of Psychology, termed Experimental or Physiological Psychology has been created to deal with the phenomena of the mind and the intellectual activities of the nervous system on an experimental basis; it applies the methods of natural science to the elucidation of the reactions of the mind to the various stimuli we receive from the external world.

**Sclerosis.** Hardening. The term applies specially to the hardening of a part from an overgrowth of connective tissue, as is the case in the hardening of the nervous elements from atrophy or degeneration with hyperplasia of the interstitial tissue. It also applies to the chronic inflammation of the arteries characterised by a thickening, hardening and loss of elasticity of their walls. The condition is then called arterio-sclerosis.

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**Sebaceous** (from the Latin *sebum*, fat). Pertaining to sebum or secreting sebum or fat. Sebaceous glands are compound saccular glands in the dermis of the skin, at the root of every hair follicle, and secreting a semi-fluid substance or sebum mostly composed of oil droplets. The Meibomian glands of the lids are modified sebaceous glands.

**Septum** (plural, septa) a partition.

**Serous Membrane.** The term applies to delicate membranes in the form of a closed sac covering the viscera, especially the heart, in which case the membrane is called the pericardium, or the lungs (the pleura), or again, the abdominal organs (the peritoneum), etc. The almost virtual cavity between the two surfaces of the closed sac forming a serous membrane is filled with a fluid formerly called serum, but which is really a form of lymph. In each serous membrane the one half of the double sac is closely adherent to the viscera it surrounds, the other half being attached to the walls of the cavity (thorax or abdomen) in which the viscera are placed.

**Serum.** The clear yellowish fluid separating from the blood after coagulation of the fibrin. The term also applies to any clear fluid resembling the serum of the blood. Thus, artificial serum is a solution containing 7.5 grammes of chloride of sodium or common salt in 1,000 c.c. of distilled water. In recent years, the term serum has been used to denote media prepared by the production of the toxin of certain bacteria, the injection of which in an individual immunises him from the disease caused by the bacteria from which the toxin has been obtained. Thus we speak of antidiphtheritic serum, of anticoryza (or antistreptoccic) serum, antityphoid serum, etc.

**Sinus.** The term sinus in anatomy has two different meanings and serves to denote a hollow, or a cavity or a pocket containing air, as is the case for the air cells of the skull, or again, more or less large channels containing blood, especially venous blood as is the case in the cavernous sinus.

**Species,** a Latin word denoting a subdivision of a genus of animals or plants, the individuals of which are either identical in character or differ only in unimportant and inconstant details.

**Stimulus.** Latin word, the plural of which is stimuli, denoting an impulse, a goad or anything capable of causing a stimulation.

**Styptic.** (See Astringent.)

**Synovia.** (See Articulations.)

**Synthesis.** A chemical term denoting the artificial formation of a compound substance by combination of its constituent elements. Thus the synthesis of water is obtained by mixing two parts of hydrogen with one part of oxygen and determining the combination of these two gaseous elements by means of an electric spark.

**Synthetic.** Appertaining to or produced by synthesis.

**Teratology** is the branch of medical science dealing with the study of monsters.

**Trabecula.** Any one of the fibrous bands extending from one part to another and the ensemble of which constitutes the loose form of connective tissue.

**Trabecular** is a term denoting the nature of a loose connective tissue, e.g., that connecting the dermis of the skin or of the mucous membrane to the subjacent structures, or the loose tissue constituting the suprachoroidal membrane.

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**Traumatism** (from the Greek *trauma*, a wound or an injury). The condition produced by a wound or an injury.

**Triton.** The name is commonly used to denote the Newt, i.e., a species of tailed Amphibian belonging to the same family as the Salamander. (See Classification of Living Beings.)

**Ulcer** denotes a loss of substance occurring mainly in the skin or the mucous membrane and due to a gradual necrosis of or death of the anatomical elements of the tissues.

**Ultra-microscope.** The optical system of the ordinary microscope has practically reached now the utmost degree of perfection. It is proved by mathematical considerations we cannot enter into, that, owing to the very nature of light, we cannot expect to see under the microscope objects the size of which is equal to or smaller than the wave-length of the light used to illuminate the preparation. As the average wave-length of white light (corresponding to the green-yellow part of the spectrum) is nearly 600 milli-microns, it follows that objects smaller than about six ten-millionths of a millimetre cannot be seen with the most perfect microscope. By using a light of shorter wave-length (violet light) the limits can be slightly lowered but, as stated before, the modern microscope has practically reached the utmost available power.

By means of the ultra-microscope it is, however, possible to detect the presence of objects the dimensions of which are below the limits of visibility, though the method does not permit to recognise the exact shape of such objects.

As a rule in a microscopic examination the preparation is illuminated by light reflected at a concave or plane mirror, travelling through the preparation itself along the tube of the instrument to the observer's eye. The field of the microscope is thus brightly illuminated and the objects examined, in order that they may be seen, must contrast with the bright field either by their relative opacity or by their coloration.

In the ultra-microscope the preparation, instead of being illuminated from below upwards or in the ordinary way, is illuminated by rays of light directed almost horizontally on the slide; these rays are reflected according to the usual laws of reflection and therefore do not pass into the tube of the microscope, the field of which remains dark. If, however, the incident rays, as they strike very obliquely the preparation on the slide, meet a particle capable of diffusing light, this particle becomes luminous and will be visible on the dark field of the microscope. It follows that in the ultra-microscope the observer does not see objects, semi-opaque or coloured, on a bright ground but sees illuminated particles on a dark ground. It is possible in this way to observe minute particles the size of which is below the limits of visibility in the ordinary microscope. We cannot go into the details of this method and it is sufficient to point out that an intense beam proceeding from a small arc lamp or some other powerful source is sent onto the preparation in such a way that the rays, though they strongly illuminate the preparation, are not reflected into the tube of the microscope.

**Uvula.** (See Pharynx.)

**Viscus** (plural viscera). Any one of the organs enclosed within one of the three great cavities of the body, namely, the cranial cavity, the thorax cavity (or chest), and the abdominal cavity.

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